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## SOME PROBLEMS OF HUMAN VARIABILITY AND NATURAL SELECTION IN CLIMATE AND CULTURE<sup>1</sup>

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What follows is essentially a survey of certain aspects of variation in man, and the possibility of selection for the requirements of climate and culture in time and space. No attempt has been made to justify my assumption that man has evolved to his present state and become differentiated into races through the processes of mutation and selection. Everyone today who works in the biological field accepts the facts of genetic change which geneticists have so assiduously discovered. I hope that my fellow anthropologists will also accept the facts of selection. Julian Huxley (1950) has recently said: "*...in the field of evolution, genetics has given its basic answer, and evolutionary biologists are free to pursue other problems.*"

While most anthropologists will admit the role of natural selection in man at a pre-cultural level, many choke at the thought that over the long period during which basic cultural traits were being acquired men were modified by selection for some of these social traits as well. Requirements of communication, courtship, and defense have done much to shape the anatomy, physiology, and behavior of fish, birds, and other mammals. Communication, courtship, and defense were vital to human survival long before men knew anything about genetics or had invented very effective tools or ornaments.

By the time human beings were culturally equipped to do very much about themselves in a deliberate as opposed to an intuitive way, man in his present form and variability was a *fait accompli*. In my opinion social anthropologists also should accept Julian Huxley's plea for freedom to pursue adaptation wherever it may lead us, in the conviction that changes which have but a slight calculable advantage win out over the period of time which even the most rapid genetic changes require. Steam-heated, germ-proof, gasoline driven culture is too new to have had an effect on human

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evolution as a total process. Cities in all their filth are only 5,000 years old, and agricultural villages less than 8,000. Allowing 4 generations to a century, these figures can be translated into 200 and 320 generations respectively. I leave it to the geneticists to calculate how much change can come about in so little time, particularly when one remembers that cities have always been fed by genetic streams from the villages, and that the villagers have always been refreshed by absorption of hunting neighbors. The vast bulk of man's adaptation to culture had been acquired before villages or cities had been invented. The kind of culture to which we are adapted can still be studied in Australia.

#### ADAPTATION IN TIME

Taking time as our point of departure, two observations immediately present themselves. One is the fact that human evolution as such became inevitable in the Pliocene. Again quoting Huxley (1954): "...by the Pliocene the possibilities of improving the predominantly physical aspects of living machinery—its mechanical and chemical efficiency—had been exhausted ...purely physiological properties had reached the possible limit of specialization; the only road out of the evolutionary impasse was by way of brain and mind."

The second observation is that evolution proceeds at vastly different rates in different organisms, hence the survival of horseshoe crabs, coelacanths, and other antique denizens of the land and sea. With this in mind it is hard to understand why human species or races of different evolutionary level should not have lived side by side at one time or another, including the present. Indeed this was what Weidenreich had in mind when he arranged the fossil men known to him in evolutionary rank without regard to absolute chronology. Every species has a time of evolving, and a time of disappearance, and the same is true of races, some of which, like the Tasmanians, disappear into the chromosomes of others.

#### ADAPTATION IN SPACE

Now for space. Every class of organism lives in a certain medium or group of media; whales in the sea, bats in the air and on shady perches, and monkeys in the trees. Most species and groups of related species of animals are limited to certain environmental ranges within their special media of land, air, or sea, and form in this range a part of the integrated ecological assemblage of living things. The same is true of man, or was during early periods. Relating space to time, we find that until recently (geologically speaking) the primates as an order have always been limited to the warmer portions of each hemisphere.

In the New World the marmosets and cebidae inhabit the tropical regions of South and Central America, and the islands of the Caribbean, and do not venture far up the slopes of the cold Andes. In the Old World this is also true of the lemuroids and tarsiers, but some of the cercopiths and apes appear hardier. Gibbons live in chilly forests in the mountains of Siam, Bar-

bary apes huddle on the bleak rock of Gibraltar in mid-winter, and langurs hop about in the snow-filled branches of the pines in the Nepalese sub-Himalayas. Even gorillas are able to withstand the lesser cold of the slopes of Ruwenzori.

This geographical survey yields one important result: the knowledge that as far back as the cercopithecoid stage our ancestors could have had a capacity for cold adaptation such as some races of living man presently exhibit. Nevertheless the known range of higher primates in the Old World, prior to the period of human expansion in middle and late Pleistocene time, followed the lee of the girdle of mountains which cuts Eurasia into a cold and a warm-to-mild half, from the Alps to the Taurus to the Zagros to the Hindu-Kush, Himalayas, and the mountains of China.

The center of this higher primate realm is Africa, the continent on which recent palaeontological discoveries have focussed the study of human origins. If man arose in Africa, as most specialists are now inclined to believe, he could not have chosen a better place, because despite its shortage of variety in latitude Africa is long on variations in altitude and precipitation. The bulk of Africa is a plateau. In Ethiopia, Kenya, and Tanganyika, just where fossil man is being found in greatest profusion, the highlands have long possessed a climate noted for its moderate nature, presenting just the stimuli needed to permit the evolution of an all-purpose ancestor of man. Grasslands, deserts, steaming rain-forests, and Mediterranean scrub forests also characterize the decreasingly Dark Continent.

More than one kind of man-like primate could well be expected to have evolved in such a provident and varied terrain, and more than one kind, apparently, did. In Europe and Asia, on the fringes of the greater primate realm, such an all-purpose man, of one kind or another, can be expected to have become somewhat cold-adapted, like some of the macacs and langurs. Heat adaptation could have taken place in parts of Africa itself, in India, and in the islands off the shore of Southeastern Asia. Man is the most heat-adapted mammal, except possibly the camel.

Much of the primary adjustment to life in different kinds of environment within this realm must have taken place during the Pliocene, a period about which we have little direct information. It must have happened to several kinds of sub-human hominids, because aside from *Homo sapiens* himself these subhuman hominids survived into the Pleistocene in two general categories, those with brains intermediate between the stages of apes and men, and those with brains of human size but sub-human proportions.

#### ZOOLOGICAL CLASSIFICATION OF MAN

According to the current usage of anthropologists the half-brained men (those intermediate in this respect between apes and men) belong to two recognized genera, *Pithecanthropus erectus* and *Sinanthropus pekinensis*. The men with brains of human size but sub-human proportions are considered to fall into several species within the genus *Homo*: e.g. *H. heidelbergensis*,

*H. neanderthalenses*, *H. rhodesiensis*, and *H. soloensis*, while for modern man, including all living races, is reserved the title *H. sapiens*.

While this classification still satisfied many physical anthropologists Weidenreich (1943), proposed that all living and fossil forms of erect men belonged to a single species, and that the generic and specific names given above should be used only for convenience. Taxonomists, working with animals and birds, have also expressed dissatisfaction. In 1950 Ernst Mayr deliberately disregarded what anthropologists had done, and reclassified the human and sub-human material on what he considered to be a purely zoological basis. He considers all seven creatures listed above to have been members of the genus *Homo*, with the half-brained men in one species, *H. erectus*, and the full-brained men in the other *H. sapiens*. *Pithecanthropus* and *Sinanthropus* become *H. erectus erectus*, and the full-brained men are designated as subspecies or races, as follows: *H. sapiens sapiens*, *H. sapiens heidelbergensis*, *H. sapiens Neanderthaliensis*, *H. sapiens Rhodesiensis*, and *H. sapiens Soloensis*.

According to Mayr's methodology an evolutionary change in brain size or brain shape implies no greater genetic shift than a change in skin color or in hair form. Taxonomically anagenetic and paragenetic changes are of equal value. However, from the ecological standpoint, the acquisition of the final anagenetic stage of *H. sapiens sapiens*' brain form led to as great a revolution in the balance of living things as did the emergence of reptiles, birds, and mammals into the biosphere, and in that sense *H. sap. sap.* initiated a new order, that of MEN, from the company of mammals.

The order of MEN, however, differs from other orders in one important respect. Other orders had proliferated into a multitude of families, genera and species. Although there has not yet been time for such an expansion in the case of man, it is hardly likely that it will take place except as man himself wills it, for man has become his own master. In his ability to change the configuration of the earth and its atmosphere man has come to rival the entire plant and animal worlds. In this sense, as Julian Huxley has suggested, man has become a kingdom, or an equivalent and (although we hope not) an antithesis to life itself. In this paper I shall use Mayr's taxonomy in principle. In practice I shall refer ordinarily to its species, subspecies, and races in commonly accepted terms.

The use of Mayr's system makes my task much less revolutionary, and simpler. Probably every anthropologist admits that living men are descended from the *H. sapiens* of the late Pleistocene in whole or in part. The inclusion of Rhodesian, Solo, and Neanderthal in this species, as subspecies or racial systems, eliminates the question of a single or multiple origin for modern man. That other strains than that of *H. sap. sap.* may exist in the genetic palettes of some of the living or recently extinct races of man ceases to be a startling thought and becomes a run-of-the-mill question.

Whether or not they participate in our queries, the single *sapiens* subspecies found in the Pleistocene are of interest to us because they may represent the tardy survival of evolutionary stages through which the entire



*sapiens* line may have passed in Pliocene times, a matter of which we have no direct evidence. Reasoning by analogy is as valid in this instance as is our comparative use of the study of surviving subhuman primates, the monkeys and apes.

#### ADAPTATION BY TECHNOLOGY

Our third dimension, technology, is also relative. The earliest implements known are the pebble tools of Uganda, dated from the beginning of the Pleistocene. In Africa itself archaeologists have already uncovered what seems to be a steady progression from split pebbles to beaked tools to hand axes to flake tools with prepared striking platforms. The next step, which was the manufacture of fine flint blades, seems to have taken place outside Africa, at some time before 30,000 years ago. Thirty thousand is the c-14 date which we are approaching in sites in Europe, Iraq, and Afghanistan, all so far unpublished, and all dependent on the use of the new gas-techniques of C-14 analysis.

All these sites are in regions outside the limits of the cold tolerance of cultureless primates as far as we now know them. The earliest blades that we know were made by men culturally as well as physiologically able to survive the cold of the last glacier. Because the use of blades and of secondary implements dependent on them patently made life in a periglacial environment possible, this gives reason to believe that the blade itself was invented in warmer regions, or in the same regions in an earlier, warmer period.

Because most anthropologists would rather talk about these things than look for them, it may be some time before the origin of blade-making will have been discovered. Anyhow, the archaeologists of Africa do not, as a group, consider that the blades which appeared there in late Pleistocene or early post-Pleistocene time were first invented there. By the time of their appearance Africa had ceased to be the focal point of human evolution, at least in a cultural sense.

Blades, with burins, other bone-working tools, and tools of bone, antler, and ivory, made it possible for human beings to move into the realm beyond the girdling mountains of the Old World once the ice had melted, and over Bering Straits into the New World. Once the ice had melted people descended from the blade-makers began cultivating plants and herding domestic animals. The progress of technology from the beginning of the Neolithic to the present period has been rapidly cumulative, as everyone knows, and during the 320 generations (more or less) that have taken place since that time one can hardly expect any radically noticeable changes to have taken place in the physical make-up of man, at least insofar as the skeletons and contemporary art representations permit us to determine. Actually the only difference that I can find between the skeleton of Crô-Magnon man, who lived 1200 generations ago and many modern Europeans is that his bizygomatic diameter exceeded his biparietal, as one finds today among living Australian aborigines, Eskimos and Fuegians. This does not

mean that Crô-Magnon had to be closely related to any of these three particular peoples, but rather that he was a heavy chewer, as they are. Man, however, is more than a skeleton. Certain changes may have taken place in response to selection for new situations produced by cultural living that an overall morphological study of the bones may not show.

These changes, particularly visceral selection, may be termed indirect results of technological advance. However, the evolution of technology over vast expanses of time, in subhuman, half-human, and sapient cultural history, has directly involved the use of the organs of perception, coordination, communication, and of the handling of materials: the eyes, ears, brain, vocal apparatus, and hands. Few can doubt that through the agency of mutation and selection these organs have passed from an earlier primate stage of anatomy, physiology, and behavior potential to their present degree of usefulness.

#### CHANGES IN MAN'S ANATOMICAL STRUCTURE

As we scan the first of these, anatomy, on the many-faceted grid of time, space, and technology, the most conspicuous fact about it that we see is its variability in gross overall size, measured by weight, mass, bulk, or whatever. Paleontologists have shown that it is usual for a successful form of life to go through a period of achieving larger bulk either until it reaches a size norm which is best for its ecological situation as a successful animal, or until it grows so large that a slight change in environment brings about its extinction, or both at once.

Among the primates the evolutionary growth of the whole body has followed the usual routine, from shrews to lemurs and tarsiers to monkeys, apes, and men. One advantage of this growth, (overlooking for the moment the special brain developments which have taken place in this order), as many have found and as Rensch (1954) has clearly stated, has been an advance in intelligence because the functioning of the brain depends on absolute as well as relative size. Another is that as man became a hunter he had to be big in order to catch and kill the animals which provided his food, and to defend himself against rival predators. The half-brained men, *Sinanthropus* and *Pithecanthropus*, had achieved the range of body mass of *Homo sapiens* in advance of the final mutation in brain size leading to modern men. The archaeological remains in the cave at Chou Kou Tien contain abundant evidence that *Sinanthropus* was a hunter.

Once a species or subspecies, which possesses a wide and climatically varied geographical area has become established at an optimum body size range, and has become, in effect, a *rasenkreis*, as defined by Rensch (1937) and by Mayr (1941), then the total mass of the organism, all else equal, follows the ecological rule of Bergmann, postulated for non-migratory and non-hibernating warm blooded animals.

This has been demonstrated by Newman for the aboriginal population of the two Americas, an ideal area for such a study because the American Indians arrived in the New World relatively late, and through a single port

of entry. Although the situation is more complicated in the Old World, both Caucasoid and Mongoloid population bands in Europe, Asia, and North Africa show similar clines, as D. F. Roberts (1953) has most recently determined.

In Africa the situation is complicated to the point of confusion by at least two external factors, as follows: Central Africa contains *discontinuous populations* of racial dwarfs, the Pygmies. These have their own size-to-temperature cline, in that the Congo pygmies are smaller than the pygmies living on the cool slopes of the mountains in Ruanda-Urundi, as Hiernaux discovered. The Negroes, a separate people, seem to have a physiological capacity to be heavier under extreme conditions of wet heat than do members of other racial stocks.

This has been shown in Brazil where in the Amazonian rain forest Negroes run heavier than either Indians or whites, and in the Tihama of Yemen where relatively large, muscular Negroes do most of the heavy work, for which the tiny white Arabs are less suited. This does not mean, however, that within the climatic zones of Black Africa the Negroes fail to follow Bergmann's rule, merely that in Africa, our home, man is so differentiated into special racial groups that each may have its optimum size for any given climatic situation, hence co-existence. This reminds one of Vavilov's observation that near the point of origin of a class of plants, many more wild varieties are to be found than on the peripheries.

A study of the complex division of living men into a number of subspecies on this basis alone leads one to wonder which way we are facing; toward a greater or lesser diversity. This is a problem that cannot be settled by contemporary documents alone, but which requires a search into the past, not only the immediate, historical past, but the geological past, leading us through what we know dimly of the Pleistocene, into the void of the Pliocene.

#### ORIGINS OF VARIABILITY

While the matter cannot be settled on present knowledge, a schedule of probabilities can be set up. It would be much easier to equate with our present knowledge the proposition that man has been becoming less differentiated through mixture since, let us say, the end of the Pleistocene, than that he has been becoming more differentiated through isolation and selection. The reason for this preference is the fact of culture, dependent on the rapid rise of technology during the very period under consideration. This preference implies, therefore, that during the Pleistocene what anthropologists call *Homo sapiens* absorbed remnant populations of *rhodesiensis*, *soloensis*, *neanderthalensis*, and perhaps yet others which the earth has not yet yielded to the picks and trowels of archaeologists.

This hypothesis, which stems from a close scrutiny of the application of Bergmann's ecological rule to living men, is basic to the interpretation of other phenomena in the fields of anatomy, physiology, and behavior. It implies that in Africa and its neighboring fringe areas of the Eurasiatic con-

tinent the species *Homo sapiens* evolved, during Pliocene and perhaps also early Pleistocene times, into a number of sub-species of which *sapiens sapiens* enjoyed the most rapid success in the mastery of his environment by cultural means. It further means that *sapiens* men, by absorbing remnants of other subspecies, acquired genes which had permitted the members of the other subspecies to survive extremes of climate, to live together under certain unusual conditions, to communicate in special ways, and to think creatively in special fashions. By a subsequent process of differential selection, the races of man as we know them today were formed, races distinguished from one another by differences in anatomy, physiology, and capacities for behavior.

The alternative to this hypothesis is that unlike his descendants of the Age of Gunpowder, *Homo sapiens* of the Middle and Late Pleistocene period killed off his more archaic rivals for ecological *lebensraum* utterly and without trace. Yet the cultural difference between a hunter armed with blade tools and one armed with flake tools must have been infinitely less than that between Englishmen armed with rifles and Australian aborigines. Neither cultural difference nor repugnance at the grotesque elf-like faces of the aborigines prevented the English from doing what wandering men have been doing with foreign women throughout recorded history. The only possible support for the alternative would be that the various subspecies of *Homo sapiens* were mutually infertile, which in view of the existing phenotypes of marginal peoples is hard to believe.

Anatomical differences between living races, being self-evident, have long been recognized. Physiological differences are only now being widely studied and plotted on the racial maps of the world because they have become vital to global warfare and other far-ranging enterprises. Differences in capacities for behavior, particularly those dealing with that composite known as intelligence, were studied much more, I believe, twenty or thirty years ago than they are now, not only because it has been found difficult to devise culture-free intelligence tests, but also because we live in a new age of national and global unification in which the knowledge of such differences is felt to be hostile to this cosmic process. In nearly every recent textbook I have seen, if the subject of racial differences in intelligence is brought up at all, it is glossed over as unimportant, despite the fact that human intelligence by itself, in Huxley's opinion, places man, who is anatomically nothing but another primate, into "a new phylum and indeed a new Kingdom..." while the possession of superior intelligence on the part of some of us has brought us all to "a critical point in the development of our planet at which the evolutionary process, as embodied in man, has for the first time become aware of itself, is studying the laws of its own unfolding, and has a dawning realization of its future guidance or control.... evolution is on the verge of becoming internalized, conscious, and SELF DIRECTING." (Huxley 1954 pp 12-13) If intelligence is as important as all this, a knowledge of its distribution among the peoples of the earth should be obtained as part of our global stock-taking, nor should we permit

the inquiry to be smothered for the purpose of maintaining equilibrium. Only from disequilibrium does progress issue.

#### VARIATIONS IN FORM

Next to mass, the second most conspicuous feature of the total organism is form. This may be expressed as the degree to which the animal resembles a sphere, or the ratio between surface area and volume. Some animals, like hedgehogs, can roll up into balls at will, others, like bees, can turn into balls by swarming together. Primates can do neither very effectively, although Bushmen in cold nights on the Kalihari sleep together in a huddle, and Chukchis in Siberia keep warm in a fur box by the combined heat of their bodies. Both these devices can be used only at rest, and each requires the use of skins as an outer covering, and this is a cultural artifact.

Both are concerned with heat regulation. As Allen long ago pointed out, one of the primary mechanisms of heat regulation in animals is heat loss through special organs. Last May, in the hot season, I spent a day riding on an elephant in the jungle of southern Siam. The elephant constantly flapped his ears, which were very thin and vascular. From time to time he regurgitated a quart or two of water from his stomach and blew it onto his belly; some of it reached his ears. The use of his ears as radiators and of his trunk as a showerbath nozzle permits so bulky an animal as an elephant to keep his body cool enough for comfort in a region of abundant water.

In many other mammals such as rabbits, the ears also serve as radiators, while in others, such as man, much of the body's heat loss is channeled through the limbs, especially the forelimbs and fingers. Nevertheless the whole body is concerned with heat regulation, and the greater the surface area in proportion to mass, the more easily can heat be lost through sweating and evaporation. This is particularly the case in arid regions where there is usually a breeze; a skinny man is at a great advantage in this sense over a rotund one. However, where the humidity is high and breeze lacking, as in most tropical forests, sweat merely bathes and drips off the skin. Shape is less important than size. Inhabitants of tropical forests are usually small people, because a small man can throw off his heat load more effectively than a large one can. (Miller and Morehouse 1953.)

Whatever their means of heat loss, animals living in deserts are usually long and lean for other reasons. During the daytime the temperature at the surface of the ground is much higher than it is a few feet above it. The higher up the bulk of the body is carried, the less the heat of the atmosphere in which it moves. Another is that long, lean, animals move more swiftly than short-~~er~~ged, rotund ones. Swift movement in hoofed mammals means the ability to reach water, and to escape predators. In predators such as the cheetah and man, swift movement means success in hunting as well. In the hundreds of thousands of years during which our ancestors were hunters and before clever men had invented the bow and tamed the dog, the men who hunted on the grasslands and deserts must have been rigorously selected



for speed, one of the chief requirements for which is a light, lean body build. As anyone who has been to Arabia knows, light lean men still inhabit the desert.

In contrast to the build of the desert Arab one may consider the short-legged, long-trunked, barrel-chested, broad-handed physique of a typical Armenian kebab-cook, let us say in Aleppo. Turn on the television late in the evening and dial for the Chicago wrestling show, and you will see a group of performers rigidly selected for a sturdy physique. They are classic Sheldonian mesomorphs, in whom the ratio of surface area to mass is much lower than in the desert dweller. A brief review of the animal kingdom produces the observation that this kind of build is typical of forest dwellers. Speed over long distances is of little use in a forest. The hunter hears an animal call or sees a track. He moves toward his prey, but in so doing he is constantly using many muscles which the desert man rarely calls into play for the purpose of locomotion. The forest hunter lifts his feet high to climb over fallen logs and pulls them out of mud; he pushes aside creepers and branches with his hands. He twists his trunk this way and that to avoid obstacles. His whole body is exercised thoroughly before he has gone a mile. The amount of energy he expends per mile for locomotion alone is many times that used by the desert hunter. A stocky, muscular build is as necessary for his survival as the greyhound body form is for that of the plainsman. If it is a cold forest he will be a big stocky man, if a hot one, a small stocky man. To the extent that both size and build are genetically controlled, primitive hunters without bows or dogs must have been selected for these characteristics.

#### VARIATIONS IN POSTURE

Another variation which concerns the whole body is posture, which in man serves both locomotion and technology. Man is the only animal that can carry things in his hands while walking, or that can strike another animal with a weapon held in the hand, while standing erect. In imitation of human beings a chimpanzee can do many things with his hands, but only after he has sat down. A hunter who did his hunting on his buttocks would soon starve.

It is easy to overlook the subject of posture in man because of the currently popular theory that man's body evolved section by section, with the posture first and the brain last. However, the pelvic form of the Australopithecines was not fully hominid, and not all authorities agree that they were fully erect. Zuckerman (1954) supports this and Clark (1954) considers them less erect than *Homo sapiens*. A belief in the erect posture of the Australopithecines was a cornerstone of the piecemeal theory of evolution, once also used to explain the inconsistencies of Piltdown.

Now the type of man to whom a fully erect posture would be necessary once he had the cultural equipment for hunting would be the man dwelling on deserts and grassy plains. The ability to balance his head over his trunk, and both head and trunk over his legs, would make it possible for him to



run faster than any ape for a long distance. In the competition for food before the days of dogs and bows and arrows, the average open-country dwelling man must have been built like Paavo Nurmi.

Yet the forest man, whose body is constantly out of balance anyhow, would find himself under less pressure to become perfectly erect, and more likely to stay the way he had been before these cultural advances had come to him. As the muscles of his neck, trunk, and arms were all concerned with locomotion the sagittal balance of his body was of less importance, and although speed in catching game was still vital, it was of the hundred yard dash type only. This may be why the bodies of neither *Sinanthropus* nor *Neanderthal* had achieved a perfect sagittal balance. Our thesis of interspecific absorption will thus explain the wide variation in head-hafting, lumbar curve, and other postural details today.

#### VARIATION IN OTHER BODY PARTS

When we consider the body components: skin, hair, bone, teeth, muscle, fat, viscera, nervous tissue, and blood, many interracial differences of a profound nature may be found. Much work is being done on this subject at present in several laboratories. Not being fully up-to-date on it, I cannot attempt a complete coverage.

Human skin varies in many ways, most of which have to do with adaptations to heat, moisture, light, and abrasion. The ratio between skin surface area and mass has been mentioned under the subject of overall proportions. The more skin per unit of mass, the easier it is to cool the body by perspiration. Variations are also found in the number of sweat glands per unit of skin area. Subcutaneous fat is most abundant in cold regions, and thick skin among people living in wet heat, where infection following abrasion has a high incidence. In Africa Hiernaux finds thick, massively wrinkled skin among pygmies; just the kind of coarse skin Sheldon specifies for his white mesomorphs. Hiernaux's (1954) observations assign thin, fine grained skin, which shows blood vessels plainly, to his long-legged Watusi and other African equivalents of Sheldon's similarly thin-skinned ectomorphs. Pigmentation of the skin is a function of exposure to light. While it is particularly concerned with protection against ultra-violet light, the capacity of black skin to absorb visible light rather than reflecting it, and to convert this light into heat, also lowers the sweating threshold of black-skinned races and thus contributes to their heat-loss efficiency.

Body hair, extremely variable quantitatively in man, both individually and by races, is cover hair, not fur. While affording little protection against cold it serves to protect the skin against light scratching. Essentially a forest adaptation, it is found mostly among pygmies, Alpines, Ainu, and the type of Australian aborigine which Birdsell calls Murrayian. I have also seen it among natives of New Caledonia. As our pre-hominid primate ancestors were no doubt hairy, the retention of hair by individuals among the peoples mentioned above merely means that, as in the case of imperfectly erect posture, its absence is not advantageous. It is rather the absence of

this covering that must be considered adaptive, on the one hand to hot dry conditions in which the surface of the skin must be free to permit the breezes to evaporate sweat, on the other to extreme cold in which protection depends rather on fatty deposits under the skin.

Unlike the body hair, which varies with environmental conditions, certain other categories of the hair cover of the human animal are relatively constant, implying universal functions. Eyelids and eyebrows are present in members of all age groups, both sexes and all races. Their protective functions are obvious. Pubic and axillary hair also protect particularly vulnerable areas, but as they are found only among adolescents and adults they may also once have played some part in courting activities, serving as brushes to preserve particularly exciting odors.

When we think of the function of head hair we must again hark back to a period when men and women were living in a state of extreme cultural crudity, when lacking mirrors or any other kind of toilet articles, they had no facilities for hair cutting or beard clipping. Their pilous appurtenances were just as functional and just as necessary for survival as those of other animals. It is hard to visualize such a cultural situation in terms of our knowledge of surviving primitive hunters. It is much easier to relate it to the lives of the very earliest members of the genus *Homo*.

Thinking in these terms we see that head hair in most races, when it is allowed to grow uncut and unfrilled, forms a protective mane over the back and sides of the neck. Now the neck is an extremely vulnerable part of the body, as anyone who has studied unarmed combat knows. One is always taught that a sharp blow with the fist on the back of an unsuspecting man's neck may snap it and kill him, that a cut with the side of the hand to the jugular may also be fatal, and a blow on the Adam's apple likewise. These tricks, which need no artifacts, may be as old as man. Professional wrestlers always carefully avoid delivering such blows, however much they may clown. In the days when necks were available to the claws and fangs of animals and the sticks and stones of subhuman enemies, such a mane was vital. Women were just as subject as men to surprise attacks from the rear. Even a bald man has enough hair in his fringe to provide some protection.

The beard supplies similar protection to the front of the neck and the face. Children and women lack it. Possession of a beard implies the will to fight, as the very glands that make a man aggressive also make his beard grow. A beard is the symbol of a human being of a sex and age who, rather than turning to flee, stands to defend himself and his family. It implies a sexual division of labor in external relations. Among some other primates comparable somatic devices are in evidence, as for example the great collar of tough skin which frames the face of the male orang like a picture frame. Both he and the gorilla have such short and muscular necks that manes are not needed.

Mongoloids lack beards which collect ice in extreme cold, and ice freezes the face. Negroids have spiral hair which leaves the neck free for heat loss. In extreme cold and extremely damp heat, thermal equilibrium is

more important than protection from blows. Where a choice between two kinds of adaptation needs to be made, nature picks the more vital of the two; or it may be in some cases that the choice is progressive; one form of adaptation fits a certain cultural level while another is better suited to a more advanced condition.

The next body component on the list, bone, is the densest of all next to the teeth, which occupy but a small part of the total. The availability of calcium and trace elements in the diet furnish the range within which bony development is possible. Large scale phenotypical changes are often seen in populations which move from one dietary area to another; compare the gauchos of Argentina to their cousins in Spain. These phenotypical changes, however, do not run against the standard ecological rules which they rather implement.

Like the gorilla, *Sinanthropus* and Neanderthal possessed long bones in which the shaft thickness was great and the marrow cavities narrow. Early gracile varieties of *Homo sapiens* ran about on long bones engineered for lightness in terms of strength, like bird bones. The dichotomy between woodsman and plainsman is clear. Among living human beings a great range of bone thickness, bone density, and ratio of sidewall to marrow cavity is present. People who live in forests and those who plod through snow have, unless I am mistaken, heavy bones, and desert dwellers and swift runners elsewhere have light ones.

Adaptation to culture may also be measured on the scale of tooth size. All else equal, the descendants of the first people to cook, and of the first to boil, may be expected to have the smallest teeth. This does not mean that lack of chewing makes teeth small, but merely that when chewing becomes less necessary than before, people with smaller teeth have a better chance of survival than they did before.

Muscle goes with bone; forest men need heavier muscles than plainsmen and desert people. The amount of muscle that one needs for hunting and carrying game varies in inverse proportion to the needs for long distance travel and to the use of the intellect in inventing labor-saving techniques. A special group of muscles that merit attention are those that operate the jaw: the temporals, masseters, internal pterygoids, and external pterygoids. In Neanderthal and Rhodesian, the temporals are strongly developed, and placed far back on the temporal and parietal bones: the ascending ramus of the mandible takes the form of a hook. The masseters are poorly developed, and the bizygomatic arch feeble, so that face breadth is less than head breadth, as in modern machine-age man. In Neanderthal the internal pterygoid, used for rotary grinding, is strong. In *sapiens* the temporals are set farther forward to accommodate the growth of the anterior portion of the skull; the ascending ramus is short, and actual muscle bundles underlie the bizygomatic arch, which is greatly bowed. The masseters are powerful. The face looks square, and it is wider than the braincase. This condition obtains in all Pleistocene *sapiens* skulls, (*sapiens sapiens* in Mayr's sense)

and in Mesolithic crania. It is still to be seen in living marginal hunters like the Fuegians and Australian aborigines, and among the Eskimo.

In my opinion the difference between broad and narrow-faced *sapiens* men (relatively to head breadth) is phenotypical, as a function of the amount of chewing done by the individual. This can easily be studied among aborigines reared on reservations and in mission stations where they have nothing more to chew than tea and soft white bread. What is not phenotypical only is the difference between the manner of attachment of the temporals in Neanderthal versus *sapiens*, the development of the masseter in the same, and the total jaw musculature. For some reason which I cannot understand *sapiens* had more powerful jaws than his Neanderthaloid cousins. One is tempted to resort to concepts of difference in muscle tone and quality, for surely Neanderthal had as much chewing to do as *sapiens*.

The component of fat includes three divisions: the essential fat that packs the eyeballs and kidneys, and is necessary in every healthy human being; omental fat, which stuffs the body cavity in pot-bellied people who may otherwise be lean; and subcutaneous fat. Present fat-caliper techniques measure only the third variety. Fat of this kind is turning out to be important as a cold-resisting mechanism. Numerous studies by the Quartermaster Corps are showing racial differences in subcutaneous fat among healthy young males; Keys, Angel, and others have been studying it on wider age and sex samples.

In Melville Island in June, 1954, I measured body fat on the aborigines and obtained the low figure of 2.38 per cent for my male sample, using the formula developed by Brozek for white men, which may or may not be fully applicable to this population. In a total population of 150 there was one fat woman, who would have appeared obese in any population, one plump woman who in our population would fail to be called skinny, and one man with omental fat. Everyone else was lean. The capacity to become fat has a low incidence on that island. Under the great heat of this environment during the monsoon season, to be skinny has survival value. The fat individuals resembled pictures I have seen of Tasmanians and natives of Victoria, where the opposite weather conditions prevail.

Under conditions of malnutrition, the body converts subcutaneous fat into sugar for its own nourishment; people starving for lack of calories are always thin. Steatopygia, as seen in Bushmen and Hottentots, is a device whereby fat may be stored without interfering with heat loss or locomotion. Rensch finds this also among fat-tailed sheep and camels. The capacity to store food in this manner must be genetically controlled.

Domestic animals in general tend to store large quantities of subcutaneous fat, at the expense of bone. Sheldon's endomorphs may be found commonly among sheep, cattle, and pigs which are bred for meat. So prevalent is this tendency that one can tell by feeling and hefting them which bones found in an early cave deposit are those of domestic, and which of wild, animals. One wonders if unqualified endomorphy in human beings, preserved through lack of selection, is a product of dependence, and how much part this

tendency may have played in the initial differentiation of the Mongoloid stock.

We move on to blood, which, according to the textbooks, comprises 9 per cent of the body weight. Dupertuis (1948) finds that ectomorphs have the most blood per unit of body weight and endomorphs the least. Viewed from the standpoint of heat adaptation alone, this would indicate that people built for sweating in hot dry climates need and have the blood to do it with; rotund fat people become most rapidly dehydrated under these conditions. The survival value to desert dwellers of a relatively high liquid content is self-evident.

A quart or more of this moisture is used daily by the nose in its task of humidifying the 500 cubic feet or so of air which it sends to the lungs. The nose not only humidifies the air that we breathe, but it also cleans it, an important function in dusty environments. In cold climates, it warms it as well, for the air must be warm in order to absorb moisture from the mucosa (Negus 1952). Among the primates which inhabit hot, wet, forests, the air is already warm, damp, and relatively clean. It was when he left the forest to live on the open plains that man's ancestor needed a nose highly efficient in these respects. The baboon, another dry-country primate, has a large nose disguised by its equally prominent jaw.

Variations in the form of the human nose reflect environmental needs. The relationship between the length-breadth index of the nasal aperture and latitude has long been known. High, narrow, prominent noses are found among both desert dwellers and people living in moderately cold regions; in regions of extreme cold the forward position of the malars and the fat pads over them help maintain the thermal equilibrium of the organ, which in all races is also useful as a part of the machinery of speech.

#### VARIATIONS IN THE BRAIN

Last and most important of all items in the anatomical equipment of human beings is that of the nervous system, and particularly of the brain. Rensch (1954), who has recently summarized the story of the evolution of the brain among mammals, finds that as a group of successfully evolving animals grows larger in body size, the brain grows absolutely larger but relatively smaller. However, the forebrain grows larger in proportion to the rest of the brain, and the frontal lobes gain in particular. In most cases the brain acquires more and absolutely larger ganglion cells, and therefore more dendrites. This increase in size means more complicated nervous connections, more plastic behavior, and an increased utilization of experience.

Animals of larger species live longer than those of smaller species, and thus have time to learn more. In hens, rodents, and fish, the larger species take more time to learn, but they learn more than the smaller ones do, remember longer and can solve more complex problems. Rensch attributes the superiority of the larger species in these respects to their greater brain volume, with its emphasis on the frontal area.



Several authors, particularly Chance and Mead (1953) and Etkin (1954) have recently produced theories to explain how certain Pliocene primates of the Old World who had achieved a measure of erect posture and had approached the threshold of becoming human, were able to take the final evolutionary step through the selective advantage of a large brain. Chance and Mead point out that the "primates in general are subject to much conflict in their social relations, that they differ from all other animals in that the particular type of social conflict is an ever-present element, and this conflict has a pronounced selective action on the breeding performance of individuals within the group, and this will have evolutionary consequences of a very high order."

In brief, they postulate that our ancestors lived in open country in groups of several families each. Unlike other primate females, the pre-human females were sexually attractive all the time, and thus unions of some permanency were formed. The males in the camp, able to see one another from family locus to locus, resolved their natural conflicts in socio-spatial terms, which means a tacit agreement to keep to their own territories. The success of the primate male in breeding depends on his success in a challenge, with bullying, and with or without a fight. Now a stupid young sub-human whose sex instincts and rage reflexes would lead him to challenge an older and stronger male over a female might get beaten or killed; a brighter one would bide his time until he had grown strong enough and imposing enough, and the exact moment had arrived. His superior judgment would be rewarded by success at breeding, and his offspring would people the plains.

The capacity for exercising such profitable restraint and that for good judgment stem from the forebrain; and experiments on cats and monkeys show that the area of concentration for the suppression of rage is centered in the amygdala, which is very highly developed in man. Further experiments, conducted by Ward, concerned the results of performing prefrontal lobotomies on macaques. If one lobe were removed, the animal's difficulties lasted about a month; if both, they became permanent. A lobotomized macaque loses social controls. His good manners disappear. Although he does not become more aggressive, he takes food belonging to others, and fails to anticipate punishment. In other words, the prefrontal lobes seem necessary in this species of monkey for good judgment, good taste, and good manners in social behavior. The inference for man could not be clearer.

Etkin carries us a stage farther to the point where primitive men are using tools and fire. The males go hunting, the women stay home to care for children and tend the fire. Like Chance and Mead, he stresses the longer oestrous period of the human female over those of her primate sisters, and he adds the loss of body hair and the addition of ventral copulation to the advantages of being human. While these factors stress the permanency of family life, the loss of hair also eliminates that favorite pastime of lower primates-grooming, for which, having developed speech, human beings sub-



stitute chatter, or talking just for the sake of interacting. Now speech becomes man's primary vehicle of interaction. The division of labor between the sexes eliminates sources of intersexual conflict, and the role of the woman as a home-body permits the longer maturation period of the offspring.

I find both these reconstructions admirable in different ways, and complementary to each other, as Etkin's paradise, whether or not he so intended it, involves a later stage than that of Chance and Mead and a more competent use of language. Three points stimulate me particularly. Chance and Mead make the presence of open ground a necessity for this kind of social and cerebral evolution; that suits exactly my concept of the locale of the evolution of *Homo sapiens*. Etkin originates the concept of a division of labor serving as a method of reducing channels of aggression. While he cites it only for the relation between the sexes, it has also served to preserve the young and the aged, men of different trades and professions within social systems, and it has made possible the great inventions and scientific discoveries of all time. Without this human mechanism for channeling aggression, as Etkin puts it, culture could not have arisen. A third point, made by both authors, concerns the amount of time man spends in sex affairs. Both stress the role of this activity in producing culture, but neither mentions the other side of the coin, the role culture plays in permitting this agreeable pastime.

Most other animals spend a minimum of time and effort in reproduction; the number of meetings per year is limited, often to one; the efficiency of the sexual act, in terms of the number of offspring per unit of mating, is high. Most animals are too busy finding their food and eluding their enemies to take much time off for sex. Furthermore mating time is the most dangerous time of the year, the time when animals, preoccupied with procreation, are most easily caught. That is one reason why we have the hunting season at the mating time of the animals we hunt. Man had to be an efficient animal living in an optimum environment, as far as food is concerned, before he could develop the human family and band system.

So much stress has been laid on the development of the forebrain, and particularly of the frontal lobes, that we are drawn back to our earlier question, the variability of living men in terms of their relationships to earlier subspecies of *Homo*. *Homo sapiens*, with his orthognathous jaws and steep forehead, has a relatively great development of the prefrontal area. Rhodesian, Soloensis, and Neanderthal, judging from the shape of their skulls and endocranial evidence, had smaller, less fully developed prefrontal areas. Among living men many of the Australian aborigines approach the level of Rhodesian and Soloensis in this respect, this has been observed on the actual brains of aborigines by Shellshear. Both Bean (1906) and Father Connolly (1950) found in American Negroes who seemed relatively African genetically, not including obviously mixed individuals, a tendency to a relatively small prefrontal region, but they took pains to add that the range overlapped that of white people's brains considerably. This situation is exactly what one expects to find in view of the evidence of human pale-

olontology and archaeology, that as *Homo sapiens* expanded within his ecological realm he absorbed remnants of other related subspecies on the way, some of the genetic features of which may still be seen in living men who have not been exposed to situations offering selective rewards in the capacities served by the anterior portion of the brain.

One subspecies, however, that *Homo sapiens* seems to have absorbed may have led him into a situation where selection of this nature was stringent. That was Neanderthal, for immediately following his absorption by *Homo sapiens* in the Near East, we find people invading the cold areas of Eurasia north of the protective girdle below which human beings had formerly existed. In France, northern Iran, and Afghanistan north of the Hindu Kush we find, around 30,000 years ago, human beings defying the periglacial cold, working skins and sewing them by means of bone awls, and making many kinds of tools on blades. Some of these men, who lived in princely fashion on the flesh of horses and other large ruminants, resembled the hybrids of Palestine in certain anatomical details (see addendum).

These men had to be energetic and hardy to survive at all, and such tasks as mammoth hunting required all of the qualities of judgment, planning, and group coordination for which the frontal areas have been found useful in lower primates. The cranial capacity of their skulls, while variable, ran about 200 cc. greater than the average for modern men, and their frontal areas were well filled. Now in the evolutionary growth of the brain among animals increasing in body size, the actual increase of the gray cells in numbers is greater than a simple function of the cubic capacity of the brain, because the cells do not themselves grow in individual size, and because the complexity of folding increases. Thus an increase of this order would imply a major increase in human brain size, something that did not come about until human beings had advanced beyond a certain point along the path of technology, and had arrived in a situation where an increase in body bulk was generally advantageous, as it is in the cold, and some selective value would attach to an even larger relative brain size than before. Individual skulls of prehistoric Bushmen have been found in South Africa with capacities approaching that of Daniel Webster, and individual Australian aborigines, in southern Australia, have been reported with immense brains. There simply was no selective advantage to brains of that size in those regions, although the population contained the same genetic variety caused by a combination of different hominid strains that gave them the plasticity, (a concept expounded several years ago by Dobzhansky and Ashley Montagu) to take the same step if occasion demanded.

A century ago, before people had grown self conscious about their bodies in a racial sense, it was the fashion for men of outstanding intellectual performance to will their brains to institutions for anatomical study. The seats of many of the great minds of the nineteenth century were thus inspected in a post mortem state. A Philadelphian, Professor Spitzka, Anatomist at Jefferson Medical School, published (1906) the results of exhaustive researches on this subject. The six brains which he personally studied would

have been seven had not an assistant, in Spitzka's absence, dropped Walt Whitman's on the floor and thrown it away. To the six he added previous studies, covering over 130 others, including the brains of Beethoven, Gauss, Daniel Webster, Turgenev, and Cuvier. Among his own six was that of Cope, whose very law had made this study pertinent. The mean cranial capacity of seventy of these which were measured for this feature was 1650 cc., similar to that of the Upper Paleolithic people of Europe, and presumably of Central Asia. Nearly all of them had highly developed, highly folded prefrontal regions, large corpora callosa, and many of them had enlarged circulatory systems, which may have been a function of age, as most of them lived long in order to attain the distinction which brought their brains to the slab of honor.

#### METABOLIC VARIATIONS IN THE BRAIN

Size, as one of my smaller-brained colleagues, who is much brighter than I am, points out, is not the only quality of a first class brain. Many a truck driver has a head the size of Bismarck's. Another factor of vital importance is the presence of at least one enzyme, in high concentration. This one is carbon anhydrase, which reaches a high concentration in primates and its highest in man. As it is concerned with the metabolism of oxygen and  $\text{CO}_2$  from the supply which the blood carries to the brain, intelligence in a broad sense is related to it, and its degree of concentration is genetically controlled, varying from species to species (Garn 1955). One is tempted to ask, what is its variability in individuals and races, and what is its relationship, if any, to brain size and brain complexity.

The blood, which carries the oxygen and sugar which feed the brain, enters a realm of extraordinary stability once it gets there. Flowing through four arteries, two on the front and two behind, it flows through a ring known as the Circle of Willis, from which arise three pairs of arteries which supply the cortex with blood. As the pressure of all four is equal, each feeds its own quadrant, but if something goes wrong one will help its neighbor through the common channel (Schmidt 1950). Whatever happens to the bloodstream outside the braincase, it maintains an even flow inside this bony castle, unless its own intellectual demands create an increased flow, which ranges from about 756 cc. per minute, at rest, to a maximum of 1300 cc. per minute, no doubt under conditions of heavy thinking. This means that man uses several times more of the body's entire blood flow for cerebration than do other animals of his size class, and an equivalent amount of blood sugar.

A large brain is thus an expensive ornament. Mental activity is more costly than muscular. From the adaptive point of view this means that man's brain size has increased from time to time as his ability to make a living has improved, in environments especially favorable for food-getting, like the vast, game-covered grasslands of the highlands of central Africa, and the windy subglacial plains of Eurasia during the last glacial period, when mammoth, bison, and horse were there to be killed in abundance. It

also means that if the circulatory system is constantly at work cooling the body through the agency of sweating, the supply of blood needed by the brain may become critical. Furthermore it is easier to keep a small head cool than a large one. Witness the extreme dolichocephaly of hot-country peoples. In regions of great cold a large head is at an advantage from this point of view, as is a round one.

A relationship may also be found between the capacity to keep on learning, brain quality, and cultural level. Among the most primitive hunters a man dies shortly after he passes his physiological peak. A capacity to keep on learning after that point is of academic but not selective interest. With cultural advances life is prolonged, and the man who can keep on learning can become a very wise man indeed, and his cerebations may be of great value to his community. While he may not produce more offspring than other men, the group to which he belongs will, and the genetic pool from which he rose will increase in numbers.

Dorland (vide Miles 1939) found in a study of 400 eminent persons that chemists and physicists produced their magna opera at 41, inventors, poets, playwrights, and dramatists at 44, novelists at 46, explorers and soldiers at 47; actors and musical composers at 48; artists and divines at 50, reformers and essayists at 51; physicians, surgeons, and statesmen at 52, philosophers at 54; astronomers, mathematicians, satirists, and humorists at 56; historians at 57; jurists and naturalists at 58. While we do not know the details of the brains of these men, it is likely that many of them are duplicated in Spitzka's catalogue.

What goes on inside these and other brains is beginning to become a little clearer to us through the efforts of the electroencephalographers. Walter (1954b) points out that the optic nerve contains about a million fibres, through which it transmits information from the eye to the visual cortex. The next step is to the nine billion or more grey cells of the rest of the brain. If each grey cell is connected by a private wire to each optic fibre, the number of connections within the brain will run to at least 9 to the 15th power, and the skull is not large enough to house that many. Walter believes that visually received messages are transmitted by scanning, after the fashion of radar, and that the alpha rhythms represent a periodic scanning, at about the flicker speed of a motion picture projector, by the cells of other parts of the brain to the visual cortex, to see what is new. Other kinds of waves represent action taken. In most normal subjects activity beyond the routine category takes place in the frontal and temporal lobes mainly when the visual pattern is novel or interesting. This, he finds, is where creative associations take place.

Aside from reasserting the importance of these areas, Walter's paper serves another purpose. It emphasizes the extreme individuality of brain wave patterns. No two people are exactly alike in this respect. Furthermore twenty percent of normal, healthy people examined have no alpha waves at all and "people with little or no alpha rhythm are the very ones in whom visual imagery is most vivid and persistent." Their action may be like that of

gunnery radar which fixes on a target, rather than TV which scans in an entirely routine fashion.

#### VARIATIONS IN COMMUNICATION ABILITY

Psychologists who use Rohrschach and other ingenious tests well know how great the variability of the human mind is in the various channels of communication. Some people, like the Arabs, are great verbalists. Their highest art is in their use of language. Russian ballet creates a profound emotional reaction without a word being spoken, Africans have attained their highest level of expression through sculpture, and Europeans probably in music, although this is debatable. Great inventors like Leonardo and Thomas Edison were not the world's greatest writers as well. Anne Roe, who made extensive psychological tests of leaders in all fields of science, including only those born and brought up in America as a control, found a great variety in verbalization, recognition of form, and mathematical ability. The one thing that she found her subjects to have in common is great energy and a capacity for hard work. The ability to communicate non-verbally is of extreme importance in the process of unifying a polyglot world.

Speaking of language leads to the consideration of a new historical tool, linguistic paleontology, devised by Robert D. Lees, and now being pursued at Columbia (vide Swadesh 1954). By a study of differences in a key set of symbols between two languages of the same stock he can tell for how many years the two peoples have been separated. Swadesh has applied this method to American Indian languages. His results for the Eskimo-Aleut languages, and different dialects of Eskimo, fit the Carbon 14 data well, and his findings for the languages of Mexico and the Southwest appear eminently likely on archaeological grounds. For example, Totanac and Yucatan Maya have been separated 6,500 years. Salishan and Quilette, on the Northwest Coast, 8,600 years. If this method can be applied to all the languages of the world, or even projected to such completely different forms of speech as the Bushman click language and tonal Chinese, certainly it will be impossible to cram all of the linguistic diversity of living man into the scant fifty thousand years of being human which some physical anthropologists will permit us.

The great variety of human speech reflects not only a tremendous time span, but also radically different ways of thinking, and is one more block in the edifice of tremendous diversification, the parent of plasticity in man. The advantage of the present reconstruction of human history over the one which makes man late to appear and derives him from a single subspecific source is that it fits every field that it touches. The temperament of a forest hunter, who has to be prepared to react suddenly to unexpected stimuli, and that of the desert man who can see long distances and needs to be able to plan his actions far in advance, could not support Sheldon more. This concept can also, if they wish it, serve the culture and personality people as a supplement to their reliance on conditioning. It may also be useful for the linguists, the Rohrschach people, and everyone concerned with the study of



human variation. What the geneticists can do with it, I await to see in some trepidation. I know that my present effort puts me out on a limb, but that is a familiar position for primates. Being out on a limb only makes a plastic, adaptable primate ready to jump to another, and perhaps higher, tree.

## SUMMARY

Natural selection has played as important a role in the evolution of man as in that of any other animal. Only when the fact of adaptation is recognized can the present racial differences in man be explained. Within the size class of living and fossil hominids, the ecological rules of Bergmann and Allen, which govern the total organism, hold; and the existing variations in the sizes, forms, and functions of different organs may be explained in terms of adaptation to the total environment, which includes culture. These organs include the brain. As an adaptation to the need of coping with increasingly complex cultural situations the brain has become increasingly efficient in a number of ways that can be measured and others, probably, which remain to be discovered. Mayr's hypothesis that all men, living and dead, of modern brain size (including Neanderthal, Rhodesian, and Solo men) are members of the species *Homo sapiens*, biologically validates the conclusion dictated by archaeological and ethnographic evidence that modern races of men are descended from more than one early form.

## ADDENDUM

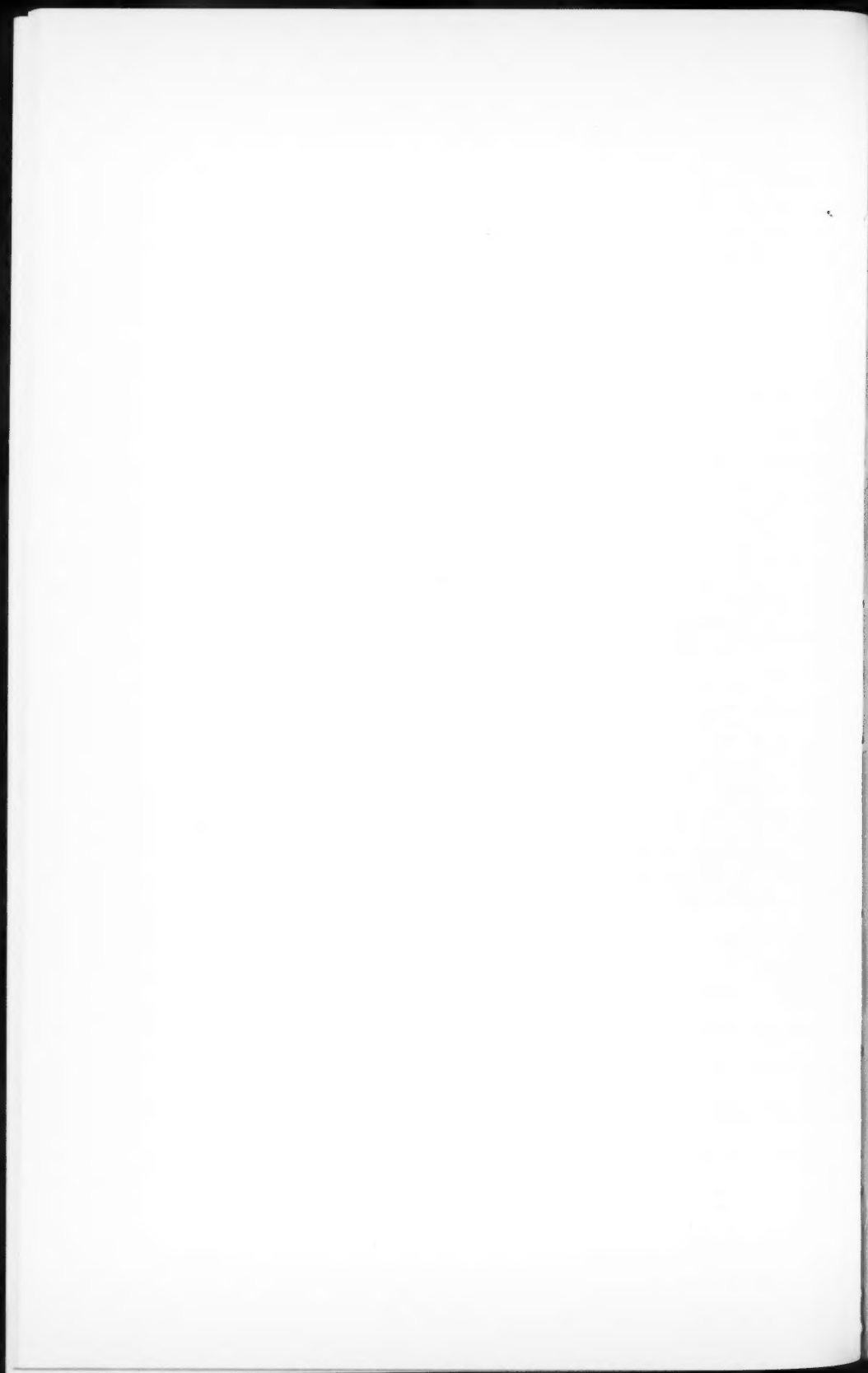
Le Gros Clark has recently (1955) pointed out that the most neanderthaloid of Neanderthals were those who lived in Western Europe during the bitter cold of the first Würm advance, while those anatomically closer to *sapiens sapiens* lived in earlier and warmer periods. To my mind this evidence indicates that the older, relatively unmixed, most cold-adapted strain clung to the edge of the cold, regardless of specific time or place, while the mixed, less cold-adapted element was to be found along the current ecological frontier between the two subspecies.

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THE STABILITY OF AN EQUILIBRIUM AND THE AVERAGE  
FITNESS OF A POPULATION

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## INTRODUCTION

Under a certain scheme of selection, a Mendelian population may reach an equilibrium condition other than complete homozygosis. The selection pressure is usually measured by the amount of change or "increment" in gene frequency ( $\Delta q = \text{new } q - \text{old } q$ ) per generation. It has been noted that certain equilibrium values of  $q$ , as given by the condition  $\Delta q = 0$ , are stable or unstable. The nature of the stability of an equilibrium may be investigated as follows:

When  $\Delta q$  is positive, the value of  $q$  is increasing; if negative,  $q$  decreasing. Assume that  $\Delta q$  is a continuous function of  $q$ , as is the case usually. Let  $a$  and  $b$  be two values of  $q$  with  $a < b$  and  $\Delta a$  and  $\Delta b$  the values of  $\Delta q$  for  $a$  and  $b$ . Then if  $\Delta a$  is positive and  $\Delta b$  is negative, there exists at least one stable equilibrium value of  $q$  in the interval  $(a, b)$ . Conversely, if  $\Delta a$  is negative and  $\Delta b$  is positive, there exists at least one unstable equilibrium in the region  $(a, b)$ . Therefore, the number and nature of the equilibrium values will be revealed by plotting the value of  $\Delta q$  against those of  $q$  in the range  $(0, 1)$ .

So far it sounds as if the stability of an equilibrium were solely determined by the expression  $\Delta q = a$  function of  $q$ . While this is undoubtedly true, it tells us very little about the meaning of a stable or unstable equilibrium except purely as an algebraic consequence of the expression for  $\Delta q$ . The primary purpose of the following sections is to view the stability from another angle—that of the average fitness of the population as a whole. Many of the points to be made have been discussed earlier by Professor Sewall Wright in connection with one subject or another. It seems, however, that stable equilibria are better understood than the unstable ones. What is the relationship between an unstable equilibrium and the fitness of the population? What does "unstable" mean in terms of the selection effect? In order to discuss these questions in the simplest manner, we begin with the case of two alleles and then proceed to examine briefly some other cases.

## TWO ALLELES, CONSTANT SELECTIVE VALUES

Let  $p$  and  $q$  be the frequencies of the alleles  $A_1$  and  $A_2$ , respectively, in a random mating population ( $p + q = 1$ ). Further, let  $w_{11}$ ,  $w_{12}$ ,  $w_{22}$  be the relative selective values of the genotypes  $A_1A_1$ ,  $A_1A_2$ ,  $A_2A_2$ , whose propor-

tions ( $f$ ) in the population are  $p^2$ ,  $2pq$ ,  $q^2$ , respectively. The  $W$ 's are assumed to be independent of the gene frequencies. Then, the average "fitness" of the population is

$$\bar{W} = \sum fW = p^2 W_{11} + 2pq W_{12} + q^2 W_{22}, \quad (1)$$

and the slope of the  $\bar{W}$  curve (with respect to  $q$ ) is

$$\frac{d\bar{W}}{dq} = \sum W \frac{df}{dq} = 2 \{-pW_{11} + (1-2q)W_{12} + qW_{22}\}. \quad (2)$$

The change in  $q$  per generation due to selection is thus (Wright, 1942)

$$\begin{aligned} \Delta q &= \frac{pqW_{12} + q^2 W_{22}}{\bar{W}} - q \\ &= \frac{pq}{2\bar{W}} \frac{d\bar{W}}{dq}. \end{aligned} \quad (3)$$

Thus, we see that with fixed values of the  $W$ 's, the equilibrium condition  $\Delta q = 0$  is equivalent to the condition  $d\bar{W}/dq = 0$ , ignoring the trivial cases  $q = 0$  or  $1$ . It follows that the equilibrium values as given by the roots of the equation  $\Delta q = 0$  correspond to a maximum or minimum point of the  $\bar{W}$  curve (1). Putting the expression (2) equal to zero and solving, we obtain (Fisher, 1930, p. 101; Crow, 1952)

$$\hat{q} = \frac{(W_{11} - W_{12})}{(W_{11} - W_{12}) + (W_{22} - W_{12})}. \quad (4)$$

This is the most general solution for equilibrium gene frequency (other than 0 or 1) in the case of two alleles. In order that  $0 < \hat{q} < 1$ , the two differences  $(W_{11} - W_{12})$  and  $(W_{22} - W_{12})$  must be both negative or both positive. In other words, for an equilibrium value between 0 and 1 to exist, the selective value of the heterozygote must be greater, or less, than that of either homozygote.

As to the nature of the stability of an equilibrium, we find

$$\frac{d^2 \bar{W}}{dq^2} = 2 [(W_{11} - W_{12}) + (W_{22} - W_{12})].$$

If this value is negative, the point (4) yields a maximum of  $\bar{W}$ . If positive, a minimum. The  $\bar{W}$  curve, as well as the values of  $\Delta q$ , for the two cases, are represented in Figures 1 and 2. Since the effect of selection is to increase the average fitness of a population, we reach the conclusion that a stable equilibrium value corresponds to a maximum point of the  $\bar{W}$  curve and an unstable value corresponds to a minimum point of the  $\bar{W}$  curve. From this viewpoint, the instability of an equilibrium becomes at once meaningful. An unstable equilibrium puts the population at a minimum fitness and the selection pressure constantly tends to raise the value of  $\bar{W}$ . Furthermore,

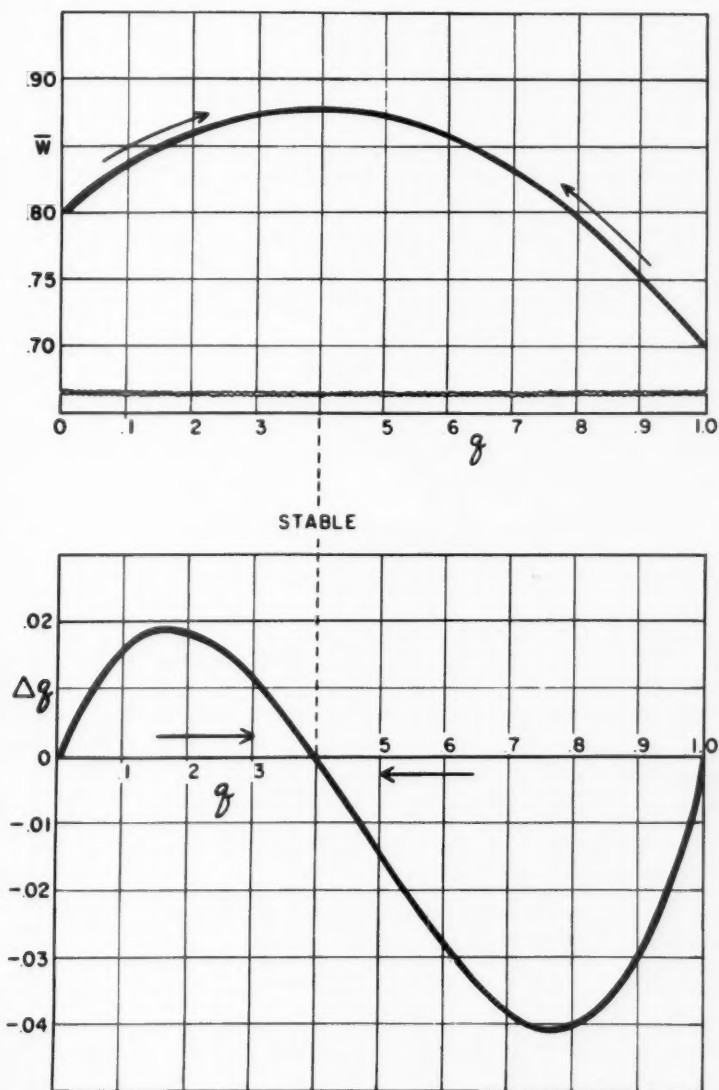


FIGURE 1. The selective values of  $AA$ ,  $Aa$ ,  $aa$  are assumed to be  $W_{11} = .80$ ,  $W_{12} = 1.00$ ,  $W_{22} = .70$ ; the average fitness of the population is  $\bar{W} = .8 + .4q - .5q^2$ . The stable equilibrium point is at  $\hat{q} = -2/(-2-3) = .40$ , which yields a maximum value of  $\bar{W}$ .

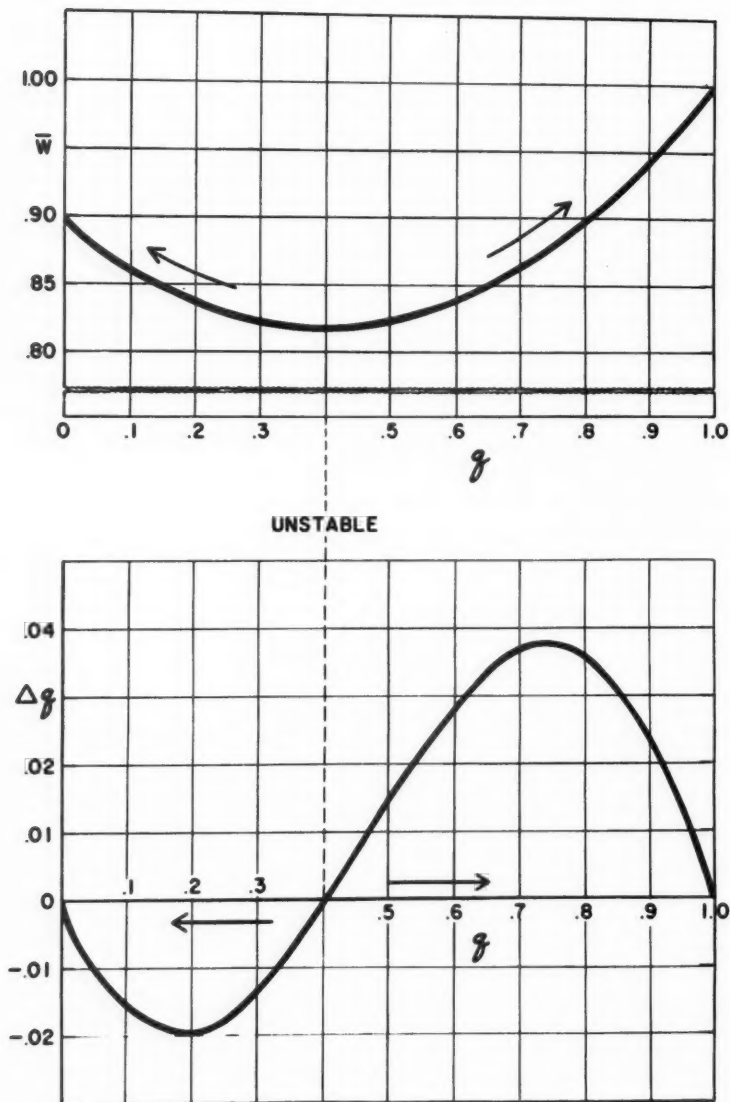


FIGURE 2. The selective values of AA, Aa, aa are assumed to be  $W_{11} = .90$ ,  $W_{12} = .70$ ,  $W_{22} = 1.00$ ; the average fitness of the population is  $\bar{W} = .9 - .4q + .5q^2$ . The unstable equilibrium point is at  $\hat{q} = 2/(2 + 3) = .40$ , which yields a minimum value of  $\bar{W}$ .



for practical investigation, the plotting of the  $\bar{W}$  curve is usually simpler than plotting the  $\Delta q$  curve. It seems that the  $\bar{W}$  curve provides us an easy and meaningful method to determine the nature of an equilibrium.

## MULTIPLE ALLELES

When there are more than two alleles, the situation becomes slightly more complicated. For the sake of simplicity and concreteness, the case of three alleles is chosen for discussion, although some obvious extensions can be made. In a random mating population let  $q_1, q_2, q_3$  be the frequencies of the alleles  $A_1, A_2, A_3$ , respectively ( $q_1 + q_2 + q_3 = 1$ ). The proportions and relative fitness of the genotypes are as follows:

	$A_1A_1$	$A_1A_2$	$A_1A_3$	$A_2A_2$	$A_2A_3$	$A_3A_3$
f:	$q_1^2$	$2q_1q_2$	$2q_1q_3$	$q_2^2$	$2q_2q_3$	$q_3^2$
W:	$W_{11}$	$W_{12}$	$W_{13}$	$W_{22}$	$W_{23}$	$W_{33}$

Here, as before, the  $W$ 's are assumed to be fixed values. Then

$$\begin{aligned}\bar{W} = \sum Wf &= q_1 (q_1 W_{11} + q_2 W_{12} + q_3 W_{13}) \\ &\quad + q_2 (q_1 W_{12} + q_2 W_{22} + q_3 W_{23}) \\ &\quad + q_3 (q_1 W_{13} + q_2 W_{23} + q_3 W_{33}) \\ &= q_1 W_1 + q_2 W_2 + q_3 W_3\end{aligned}\quad (5)$$

where  $W_1 = q_1 W_{11} + q_2 W_{12} + q_3 W_{13}$  may be defined as the weighted fitness of the allele  $A_1$ , etc. Taking  $q_3 = 1 - q_1 - q_2$ ,  $\bar{W}$  describes a surface over the  $q_1 q_2$ -plane. The partial derivatives of  $\bar{W}$  with respect to  $q_1$  and  $q_2$  are:

$$\frac{\partial \bar{W}}{\partial q_1} = 2(W_1 - \bar{W}), \quad \frac{\partial \bar{W}}{\partial q_2} = 2(W_2 - \bar{W}).\quad (6)$$

On the other hand, the increments of gene frequencies are (Wright, 1949):

$$\Delta q_1 = \frac{q_1}{\bar{W}} (W_1 - \bar{W}), \quad \Delta q_2 = \frac{q_2}{\bar{W}} (W_2 - \bar{W}).\quad (7)$$

Thus, the set of equations  $\Delta q_i = 0$  is equivalent to the set  $\partial \bar{W} / \partial q_i = 0$ , both yielding the solution  $W_1 = W_2 = W_3 = \bar{W}$ . It follows that the equilibrium values ( $\hat{q}_1, \hat{q}_2$ ) correspond to maximum or minimum points on the  $\bar{W}$  surface.

The values of  $\hat{q}_1$  and  $\hat{q}_2$  are functions of the  $W$ 's. Writing out the equilibrium equations, we obtain immediately

$$\hat{q}_1 = \frac{D_1}{D}, \quad \hat{q}_2 = \frac{D_2}{D},\quad (8)$$

where

$$\begin{aligned}
 D &= \left| \begin{array}{cc} (W_{33} - W_{13}) + (W_{11} - W_{13}), & (W_{12} - W_{23}) + (W_{33} - W_{13}) \\ (W_{33} - W_{23}) + (W_{12} - W_{13}), & (W_{22} - W_{23}) + (W_{33} - W_{23}) \end{array} \right| \\
 &= \left| \begin{array}{cc} W_{33} - W_{13}, & W_{12} - W_{23} \\ W_{33} - W_{23}, & W_{22} - W_{23} \end{array} \right| + \left| \begin{array}{cc} W_{11} - W_{13}, & W_{33} - W_{13} \\ W_{12} - W_{13}, & W_{33} - W_{23} \end{array} \right| + \left| \begin{array}{cc} W_{11} - W_{13}, & W_{12} - W_{23} \\ W_{12} - W_{13}, & W_{22} - W_{23} \end{array} \right| \\
 &= D_1 + D_2 + D_3
 \end{aligned}$$

These are identical with the expressions given by Levene, Pavlovsky, and Dobzhansky (1954, p. 342), despite their apparent different forms. The expressions (5), (6), (7), (8) of this section are analogous to (1), (2), (3), (4), respectively, of the previous section.

In the special case that all heterozygotes have the same fitness ( $W_{12} = W_{13} = W_{23} = 1$ ) but homozygotes have a lower fitness value of  $W_{11} = 1 - s_1$ , we have the stable equilibrium, corresponding to a maximum point of the  $\bar{W}$  surface. The value of  $q_1$  is

$$q_1 = \frac{\left| \begin{array}{cc} s_1 & 0 \\ s_1 & s_2 \end{array} \right|}{\left| \begin{array}{cc} s_1 + s_1 & s_1 \\ s_1 & s_1 + s_2 \end{array} \right|} = \frac{s_1 s_2}{s_1 s_2 + s_1 s_1 + s_1 s_2} = \frac{\frac{1}{s_1}}{\frac{1}{s_1} + \frac{1}{s_2} + \frac{1}{s_1}}, \quad (9)$$

in agreement with the results of Wright (1949). Conversely, if  $W_{11} = 1 + s_1$  and  $W_{1j} = 1$ , the equilibrium point has the same value but the point is a minimum of the  $\bar{W}$  surface and therefore the equilibrium is unstable.

It may also be shown that if a heterozygote (say,  $A_1 A_2$ ) is not only superior in selective value to all homozygotes but also much superior to all other heterozygotes (i.e.  $W_{12} > 1 + 2 s_1$ ), the population will eventually reach an equilibrium involving only alleles  $A_1$  and  $A_2$ ; the others will be eliminated (Wright, 1949, p. 372).

#### DIFFERENTIAL LOCAL SELECTIONS

Next, let us consider a large random mating population of which various portions are subject to differential selections. This is the case when more than one ecological niche is available in the area occupied by the population (Levene, 1953). Suppose that there are  $k$  types of niches or localities in the area, and each type has its own selection scheme. We assume, as did Levene, that after selection the survivors from the various niches form one random mating population, so that in the next generation the initial zygotic frequencies in each niche are all the same, viz.,  $p^2$ ,  $2pq$ ,  $q^2$ , where  $q$  is the gene frequency of the entire population. Let  $W_{11}^{(i)}$  be  $W_{11}^{(i)}$ ,  $W_{22}^{(i)}$  be the genotypic values in the  $i$ -th niche,  $\bar{W}_i$  be the average fitness of this niche, and  $c_i$  the proportion of the total survivors to be found in this niche

( $\sum c_i = 1$ ). Hence, after selection, the net total change in  $q$  for the entire population is

$$\Delta q = c_1 \Delta q_1 + \dots + c_k \Delta q_k \quad (10)$$

where  $\Delta q_i$  is the change in  $q$  in the  $i$ -th niche. Now for each niche, our fundamental formula (3) holds. Thus,

$$\Delta q = \frac{q(1-q)}{2} \left[ \frac{c_1}{\bar{w}_1} \frac{d\bar{w}_1}{dq} + \dots + \frac{c_k}{\bar{w}_k} \frac{d\bar{w}_k}{dq} \right]. \quad (11)$$

On the other hand, if we define the average fitness of the entire population as,

$$\bar{w} = \bar{w}_1^{c_1} \bar{w}_2^{c_2} \dots \bar{w}_k^{c_k}, \quad (12)$$

then

$$L = \log \bar{w} = c_1 \log \bar{w}_1 + \dots + c_k \log \bar{w}_k. \quad (13)$$

Hence,

$$\Delta q = \frac{q(1-q)}{2} \frac{dL}{dq}. \quad (14)$$

This is a general form of the expression given by Levene (1953) except that our  $q$  is his  $1-q$ . When there is only one type of selection scheme for the entire population, (14) is identical with (3). Here, the equilibrium condition  $\Delta q = 0$  (other than trivial cases) implies that  $dL/dq = 0$ , which, in turn, implies that  $d\bar{w}/dq = 0$ . It follows that the equilibrium points, if existent, correspond to the maximum or minimum points in the  $\bar{w}$  (or  $L$ ) curve.

Two simple examples are given here to illustrate the various possibilities of such a selection scheme. One is taken from Levene (1953). Suppose that there are only two types of niches, in one of which the genotypic selection values are 2, 1, 1.1; and in the other, .5, 1, 1.1, so that  $\bar{w}_1 = 2 - 2q + 1.1q^2$  and  $\bar{w}_2 = .5 + q - .4q^2$ . For the sake of simplicity, let us further assume that the survivor proportions  $c_1 = c_2 = 1/2$ ; thus,  $\bar{w} = \sqrt{\bar{w}_1 \bar{w}_2}$  which is plotted in Fig. 3 together with corresponding values of  $\Delta q$ . It is seen that  $\hat{q} = .40$ , the stable equilibrium point, corresponds to a maximum point of the  $\bar{w}$  curve, while the unstable point  $\hat{q} = .65$  corresponds to a minimum point of the  $\bar{w}$  curve.

As a second example, we may assume that in one set of niches the genotypic selection values are .5:1:1.5, and in the other 3:1:3, so that  $\bar{w}_1 = .5 + q(1-q)$  and  $\bar{w}_2 = 3 - 4q(1-q)$ . As before, taking  $c_1 = c_2 = 1/2$ ,  $\bar{w} = \sqrt{\bar{w}_1 \bar{w}_2}$  which is plotted in Fig. 4. Here there are two stable equilibrium values at  $\hat{q} = .146447$  and  $\hat{q} = .853553$ , and an unstable point at  $\hat{q} = .50$ . An example with three niches has been given by Li (1955, p. 265).

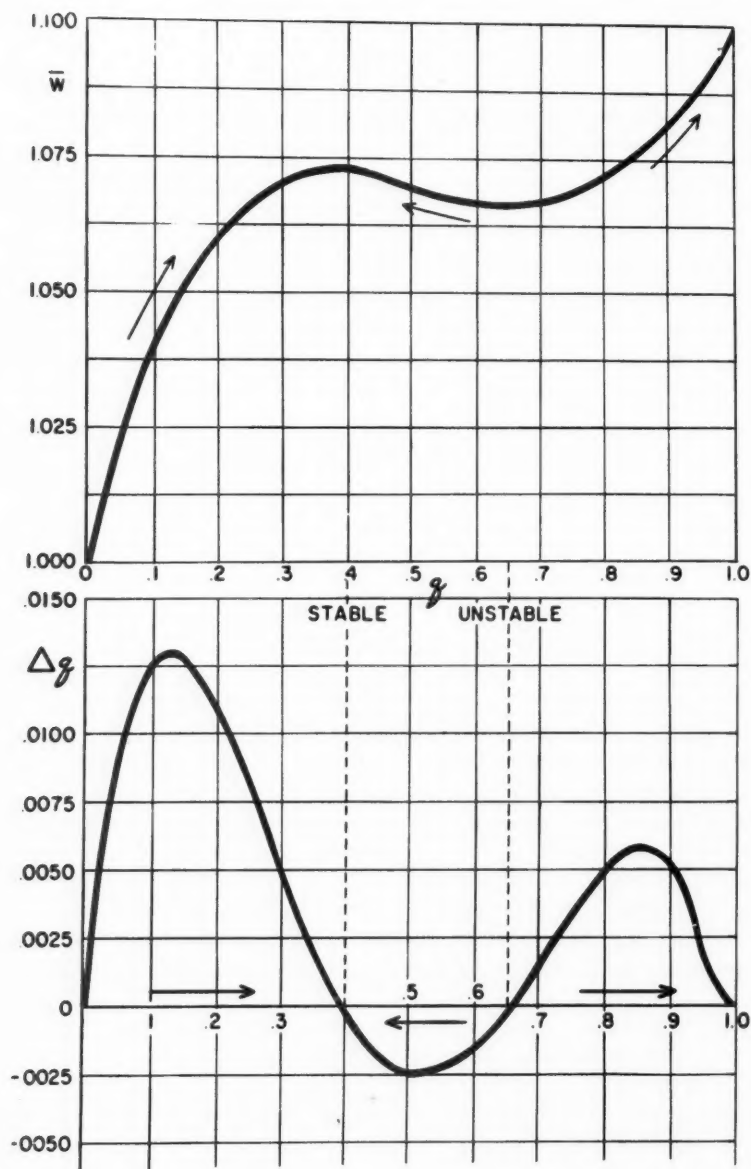


FIGURE 3. The genotypic selective values in one ecological niche are 2, 1, 1.1, and in the other .5, 1, 1.1. The average fitness of the entire population, assuming survivors from each niche to be equally numerous, is  $\bar{W} = \bar{W}_1^2 \bar{W}_2^2$ . The stable equilibrium point is at  $\hat{q} = .40$ , yielding a maximum value of  $\bar{W}$ , and the unstable point is at  $\hat{q} = .65$ , yielding a minimum of  $\bar{W}$ .

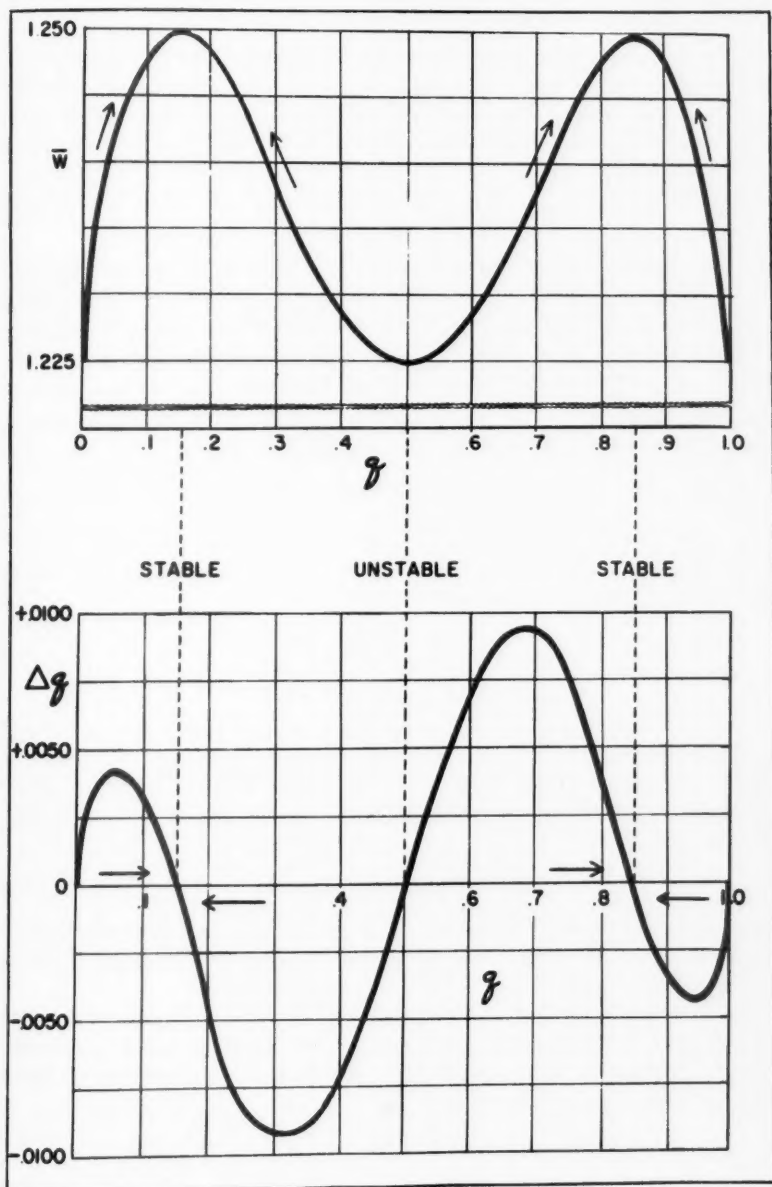


FIGURE 4. The genotypic selective values in one ecological niche are .50, 1.00, .50, and in the other 3, 1, 3. The average fitness of the entire population, assuming survivors from each niche to be equally numerous, is  $\bar{W} = \bar{W}_1^{1/2} \bar{W}_2^{1/2} = [(.50 + pq)(3 - 4pq)]^{1/2}$ . The two stable points are at  $\hat{q} = .15$  and  $.85$  approximately and the unstable point is at  $\hat{q} = .50$ .



## VARIABLE SELECTIVE VALUES

In some cases, probably more often than we thought in natural populations, the genotypic selective values ( $W_{11}$ ,  $W_{12}$ ,  $W_{22}$ ) are functions of gene frequencies themselves. In such a case our previous formulas no longer hold. If we still define the average fitness of the population as  $\bar{W} = \sum fW$ , then

$$\frac{d\bar{W}}{dq} = \sum W \frac{df}{dq} + \sum f \frac{dW}{dq}. \quad (15)$$

Note that the term on the right,  $\sum f(dW/dq)$ , is the average value of  $(dW/dq)$  of the various genotypes in the population and thus may be written  $(d\bar{W}/dq)$ . It measures the average effect of changing gene frequencies on the genotypic selective values (Wright, 1949, p. 375). This term of course vanishes when the  $W$ 's are constants, whereupon (15) reduces to (2).

On the other hand, proceeding the same way as in deriving (3) and still assuming panmixia, we obtain (Wright, 1942, 1949)

$$\Delta q = \frac{q(1-q)}{2\bar{W}} \sum W \frac{df}{dq}. \quad (16)$$

It is noted that the equilibrium condition  $\Delta q = 0$  here no longer implies that  $d\bar{W}/dq = 0$ ; but, instead, implies that

$$g(q) = \sum W \frac{df}{dq} = \frac{d\bar{W}}{dq} - \left( \frac{d\bar{W}}{dq} \right) = 0. \quad (17)$$

In words this equation says: the equilibrium value of gene frequency should be such that its effect on the average fitness of the entire population is balanced by its average effect on the individual selective values. If we regard the  $W$ 's as constant in any particular instant and define the average fitness as

$$G(q) = \int g(q) dq + \text{constant}, \quad (18)$$

then again the equilibrium values of  $q$  will correspond to the maximum or minimum points of the  $G$  curve, depending upon whether they are stable or unstable.

As an example we may cite the case of selection against heterozygotes born to recessive mothers with respect to the Rh locus in man. If the recessive mothers tend to compensate their loss by having more children (Glass, 1950), then we have (Li, 1953)

$$W_{11} = 1, \quad W_{12} = 1 - \frac{1}{2}sq, \quad W_{22} = 1 + tq(1-q)$$

where  $s$  and  $t$  are positive fractions, denoting the selection and compensation coefficients, respectively. Here

$$g(q) = -sq + 2(s+t)q^2 - 2tq^3, \quad (17')$$

$$G(q) = 1 - \frac{1}{2}sq^2 + \frac{2}{3}(s+t)q^3 - \frac{1}{2}tq^4. \quad (18')$$

When the  $G$  curves are plotted, it will be found that the unstable equilibrium values of  $q$  tabulated by Li (1953) are their minimum points.

#### POPULATIONS WITH INBREEDING

The genotypic frequencies of a population with an inbreeding coefficient  $F$  are  $(1-F)p^2 + Fp$ ,  $2(1-F)pq$ ,  $(1-F)q^2 + Fq$ . The average fitness of the population is thus

$$\bar{W} = (1-F)\bar{W}_R + F\bar{W}_I, \quad (19)$$

where  $\bar{W}_R$  is the same as expression (1) and is the average fitness of the random component of the population, and  $\bar{W}_I = pW_{11} + qW_{22}$  is the average fitness of the inbred component. The corresponding expression for  $\Delta q$  has been given by Wright (1942, 1949) and need not be repeated here. Suffice it to observe that the condition  $\Delta q = 0$  does not imply  $d\bar{W}/dq = 0$ . However, if we give double weight to the selection effects on the inbred homozygotes and define a new average fitness as

$$\bar{W}' = (1-F)\bar{W}_R + 2F\bar{W}_I, \quad (20)$$

then the condition  $\Delta q = 0$  implies that  $d\bar{W}'/dq = 0$ ; and the equilibrium point corresponds to the maximum or minimum point of the  $\bar{W}'$  curve. The situation is similar to those shown in Figs. 1 and 2. Only the equilibrium value of  $q$  now becomes

$$\hat{q} = \frac{(1-F)(W_{11} - W_{12}) + F(W_{11} - W_{22})}{(1-F)[(W_{11} - W_{12}) + (W_{22} - W_{12})]} \quad (21)$$

Note that when  $W_{11} = W_{22}$ ,  $\hat{q} = 1/2$ . Generally, in order that  $\hat{q}$  be a positive fraction, not only the two differences  $(W_{11} - W_{12})$  and  $(W_{22} - W_{12})$  should be both positive or both negative, as noted before, but the inbreeding coefficient should be

$$F < \frac{W_{22} - W_{12}}{W_{11} - W_{12}} \quad \text{or} \quad < \frac{W_{11} - W_{12}}{W_{22} - W_{12}}, \quad (22)$$

depending upon which is a proper fraction.

#### SELECTION AND MUTATION

The effect of mutation on the equilibrium values of  $q$  has been discussed by Wright in various papers. Only a few remarks will suffice for the sake of completeness of our discussion. If  $\mu$  is the mutation rate of allele  $A$  to  $a$ , then

$$\Delta q = \mu(1-q) + \frac{q(1-q)}{2\bar{W}} \frac{d\bar{W}}{dq} \quad (23)$$

The equilibrium value of  $q$  here does not exactly correspond to a maximum point of the  $W$  curve but is very close to it on account of the small term involv-

ing  $\mu$ . As a simple example, suppose that  $W_{11} = W_{12} = 1$ ,  $W_{22} = 1 - s$ , so that  $\bar{W} = 1 - sq^2$ , then, when  $\Delta q = 0$ , we obtain  $\hat{q} = \sqrt{\mu/s}$ . At this point,  $\bar{W} = 1 - s(\mu/s) = 1 - \mu$ , instead of 1. In general, the equilibrium point deviates from the maximum or the minimum point of the  $\bar{W}$  curve (or surface) only by a distance of the order of magnitude of the mutation rate. Except for this small deviation, the general situation is much the same as in the previous cases.

#### DISCUSSION

From the above analysis it should be clear that equilibrium in a population is a consequence of the genotypic selective values of the population. The method adopted involved a study of the manner in which gene frequency changes from generation to generation and the ultimate genotypic composition of the population under a given selection scheme. To compare the "adaptiveness" of one population with another is entirely another problem. In fact, the absolute values of  $W_{11}$ ,  $W_{12}$ ,  $W_{22}$ , and  $\bar{W}$  are quite irrelevant in this type of analysis. As long as their *relative* magnitudes remain the same, they yield the same values of  $\Delta q$  per generation (Li, 1955, p. 273). These  $W$ 's may thus be called the "intra-population genotypic selective values." It is meaningless to say that a population with  $\bar{W} = 1.50$  is "better" than one with  $\bar{W} = .95$ , when  $\bar{W}$  is defined the way we did. Our model for differential local selections illustrates this point very well. In that section, intra-niche comparisons were considered (Levene, 1953) and not the absolute viabilities in the different niches. Furthermore, the absolute number of survivors in the different niches is also irrelevant when the proportions ( $c_i$ ) of survivors contributed by each niche to the total population are used.

It should also be clear that the words "maximum" and "minimum" are conventional mathematical terms and have no connotations of value judgment. A population in a stable equilibrium state, attaining a maximum value of  $\bar{W}$ , does not at all mean that the population is "the best on earth." By the same token, an unstable equilibrium population (if existent) with a minimum value of  $\bar{W}$ , is not to be taken as a very "poor" population. It is just a mathematical method to describe the nature of the stability of an equilibrium. All it means is that under the given selection scheme, the population will be at a standstill at that particular point and no further change is expected under the same circumstances. To my understanding, when Dobzhansky (1951, p. 123) says "the adaptive value ( $\bar{W}$ ) of the whole population under balanced polymorphism can be shown to reach the highest level when the equilibrium proportions of the competing variants,  $q = s_2/(s_1 + s_2)$ , are established," he is referring to a situation shown in our Fig. 1, in view of the definitions he set on p. 116. Perhaps he should have added that this is strictly an intra-population business.

If the  $\bar{W}$  curve or surface assumes a complicated form with several maxima and minima, it is even possible that one "minimum" point may be actually higher than at least one of the "maximum" points on the same  $\bar{W}$  scale; yet

the populations at the (lower) maximum point will be stable and that at the (higher) minimum point will be unstable. From this view-point, one could object to Dobzhansky's wording, such as "the highest level." Even when a population occupies a maximum point, it still does not mean that it is at the highest of all the maximum points available in the  $\bar{W}$  curve or surface. Sewall Wright has explained this aspect of equilibrium repeatedly in various papers. Dobzhansky could be defended on the ground that he is referring to the case where only one stable equilibrium point exists.

However, despite the somewhat loose language used by Dobzhansky and the fact that some of his sweeping assertions have not been well established by experimental evidence, the writer fears that Cain and Sheppard (1954) have some misunderstanding about the nature and limitations of the current methods of selection analysis. Some of their arguments are semantic, concerned with the meaning and usage of certain words. In this paper the writer is also guilty of using "fitness" and "selective value" synonymously, but has succeeded in avoiding the word "adaptive." Although one word is as good as another, when it is precisely defined, a standardization of the terms and avoidance of loose language would be desirable, especially in a subject like ours.

With respect to the statement: "When there is balanced polymorphism, with heterozygotes at an advantage, in a population, the average adaptive value ( $\bar{W}$ ) of the population is at a maximum when equilibrium is reached. Consequently selection acts in such a way as to produce the maximum adaptive value in the population," Cain and Sheppard (1954, p. 321) commented: "This wording *certainly* suggests that a population in genetic equilibrium with heterozygotes at an advantage is in some way *highly adapted*" (*italics mine*). This one comment suffices to show how deeply Cain and Sheppard misunderstood the analytical method employed in gene frequency analysis. Their whole discussion seems to have stemmed from this fundamental misapprehension. The fact is that the above statement is not only true as it stands, but it could be made much more general.

If the expression "adaptive value" is as misleading as claimed by Cain and Sheppard, the writer wishes to point out that Fisher (1930, p. 100), in describing the same phenomenon, has employed the same phraseology—"that is, if the heterozygote is either better or worse *adapted* than both the homozygotes." The only thing that has escaped the attention of Fisher is the relationship between  $\Delta q$  and  $d\bar{W}/dq$ .

It should be noted that Cain & Sheppard at times seem to realize that the method applies only to intra-population selection. "The behavior of genotypes competing in the same population gives no direct evidence on the ability of separate populations each homozygous for one of the alternative genotypes, to survive in the wild" (p. 323). With this the writer of course fully agrees. In addition to the example of rapidly growing larvae versus slower growers cited by them, one may add the familiar example of Rh selection in man. The frequency of the rh allele is increasing or decreasing in

the American population, depending upon the selection scheme, but no one ever even hinted that a population of homozygous Rh negatives would be in any respect better or worse than a population of homozygous Rh positives. The important point is that when both alleles are present in a population, there will be selection effect; that is, one or the other allele will be at a "disadvantage," so to speak. There can be no selection in the absence of alternatives.

Cain and Sheppard, however, continued: "On the other hand, a particular homozygote may be at an extreme disadvantage because of extensive dislocations of its structure, irrespective of what genotypes may be co-existing with it in the same population. In this situation the selection coefficient relative to other genotypes does give a rough measure of the homozygote's chances of survival in pure cultures." This shows that their grasp of the intra-population selection concept is somewhat incomplete. The truth is "No, not even in this situation." Should man become a one-legged animal, we cannot be sure that mankind will perish from earth when raised "in pure cultures."

As to the example of *Primula vulgaris* (Cain and Sheppard, p. 322) in which a gene is of selective advantage in the gametic stage and of disadvantage in the zygotic stage, a stable equilibrium is also possible (Li, 1955, p. 264).

With respect to the association between abundance and variability of a species, Dobzhansky is inclined to think that greater variability leads to greater abundance, while Cain and Sheppard think that "greater polymorphism of the more widely ranging forms could be the result, not the cause, of the range inhabited." The writer is certainly unable to say anything definitive except to point out that, like other evolutionary factors, there may not be a fixed rule as to which is invariably the cause and which the result. It is not impossible that the cause-and-effect relationship may be reversed from one case to another. Also, there could be a chain process: viz. variability leads to abundance, which in turn leads to greater variability, and so on. It is hoped that critical experiments may be performed to shed more light on this important subject.

#### SUMMARY

The effect of intra-population selection on gene frequency in a large random mating population has been examined. In the absence of other forces when the genotypic selective values are independent of gene frequencies, a stable equilibrium value of gene frequency yields a maximum value of the average fitness of the population and an unstable equilibrium yields a minimum average fitness. This relationship is best illustrated by plotting both the  $\bar{W}$  curve and the  $\Delta q$  curve on parallel  $q$  axis of the same scale. In more involved cases, it is often possible to define a modified average fitness of the population so that the above conclusion holds.

Only relative magnitudes of the intra-population selective values are relevant. It was emphasized that they cannot be used as a basis for com-

parison between two separate populations under two different environments. A comparison of absolute adaptiveness of two populations cannot be done until "absolute adaptiveness" is defined and measured.

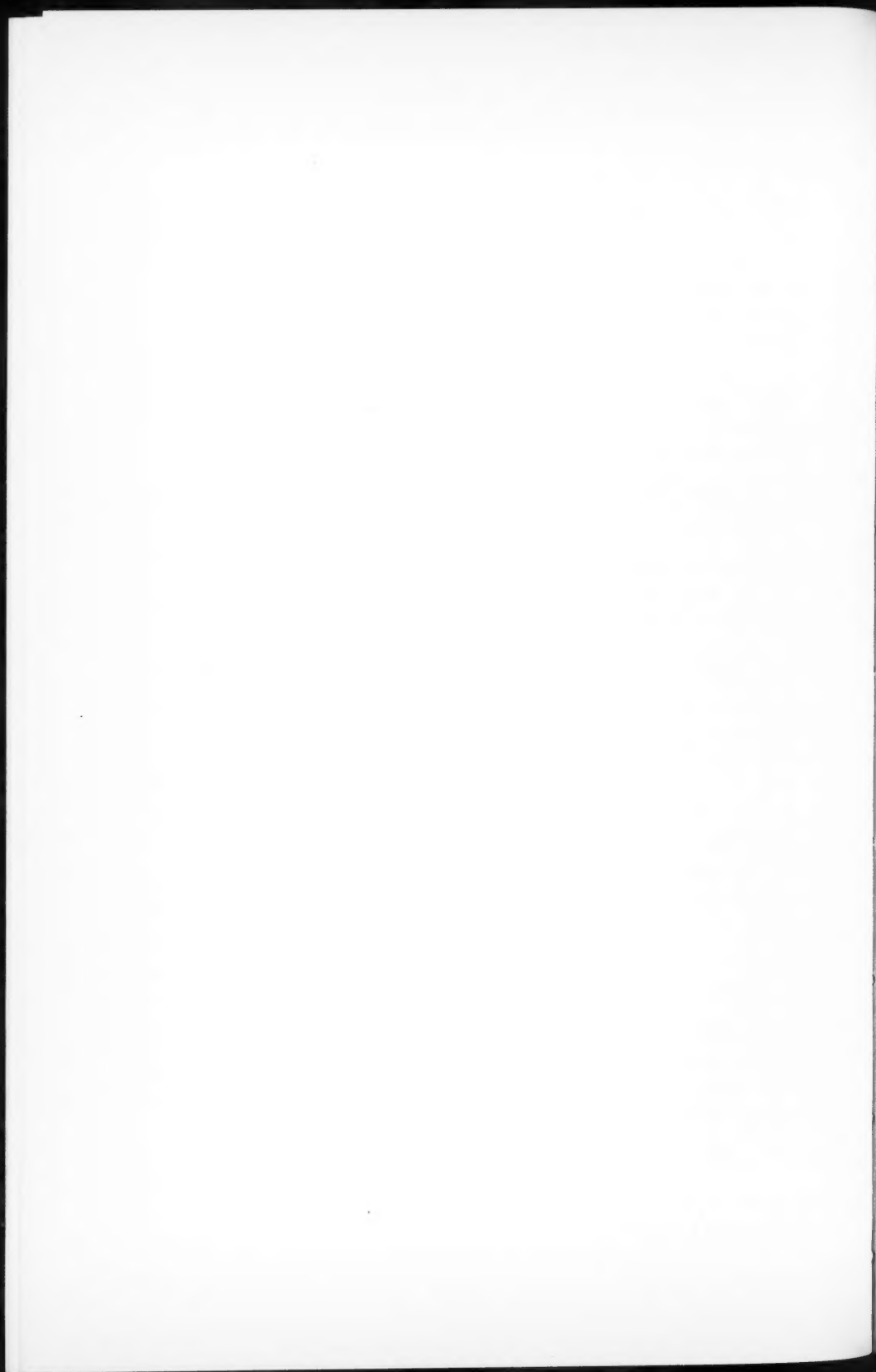
#### ACKNOWLEDGEMENT

I am very grateful to Professor Howard Levene for reading the manuscript and checking the formulas.

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SIZE DIFFERENCE AS A POSSIBLE ISOLATION MECHANISM  
IN MICROHYLA<sup>1</sup>

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## INTRODUCTION

Difference in body size may be a partially effective isolation mechanism in anuran amphibians. Failure of the male to successfully clasp the female of a larger or smaller species would tend to prevent interspecific matings. A. P. Blair (1950) has suggested that reluctance of male *Microhyla carolinensis* to clasp the smaller females of *M. olivacea* is an incomplete isolation mechanism where these species occur together. The ranges of the two species overlap in a strip running from the Gulf of Mexico in Texas north into northeastern Oklahoma. Limited hybridization occurs in the overlap zone (Hecht and Matalas, 1946), but a complex of isolation mechanisms, including differences in mating call, operates to restrict the amount of interspecific hybridization (W. F. Blair, 1955).

The present work represents one phase of a study of interspecific gene exchange between the two species of *Microhyla*. It was undertaken in part because of the contradiction between my own impression of a considerable size difference between the two species and the conclusion reached by Hecht and Matalas (1946) that the size difference between the two is negligible.

## MATERIAL

The material examined consists mostly of preserved specimens in the Texas Natural History Collection at The University of Texas. For access to additional specimens from Florida I am indebted to John S. Mecham. Measurements of snout-vent length were made with vernier calipers by David Pettus, who served as research assistant on the project. Individuals which had been distorted in preservation were forcibly flattened for measurement.

Most of the specimens examined had been collected in breeding aggregations, so they were known to be sexually mature. Mature males were easily recognized by their secondary sex characters of colored throat or distended throat skin. Separation of mature females from immature individuals was more difficult because of their lack of secondary sex characters. Obviously immature individuals were excluded, and doubtful ones were opened and checked for the presence of eggs in the ovaries or oviducts.

A total of 659 specimens of the two species have been measured. The males far outnumber the females (Table 1) because most specimens were

<sup>1</sup>This work was done under National Science Foundation Project No. NSF G-328.

collected in breeding aggregations, where males are more numerous, or at least more easily found, than females.

#### COMPARISONS

For purposes of comparing species and comparing sexes, *olivacea* from west of the overlap zone are treated as one sample, and *olivacea* from the overlap zone are pooled as another; *carolinensis* from the overlap zone comprise one sample, and those from east of the overlap zone in Texas, Oklahoma and Louisiana are lumped as another. Specimens from Florida are treated as another sample (table 1; fig. 1). For checking geographic trends, samples of males are pooled on a county basis (table 2; fig. 2).

TABLE 1.  
COMPARISON OF SIZE (SNOUT-VENT LENGTH) IN *MICROHYLA OLIVACEA* AND  
*M. CAROLINENSIS*.

Samples	Males		Females	
	Number of individuals	Snout-vent length with standard error	Number of individuals	Snout-vent length with standard error
<i>olivacea</i> , west of overlap zone	285	24.14 $\pm$ 0.12	56	27.41 $\pm$ 0.33
<i>olivacea</i> from overlap zone	145	23.42 $\pm$ 0.14	27	25.96 $\pm$ 0.28
<i>carolinensis</i> from overlap zone	35	26.66 $\pm$ 0.42	17	29.35 $\pm$ 0.66
<i>carolinensis</i> , east of overlap zone	60	27.35 $\pm$ 0.41	23	28.14 $\pm$ 1.33
<i>carolinensis</i> , Florida	16	23.44 $\pm$ 0.22	11	25.91 $\pm$ 0.58

#### BETWEEN SEXES

Males of *olivacea* are distinctly smaller than the females (fig. 1). Overlap-zone males of *carolinensis* and those from Florida are smaller than females. On the basis of the small samples available, there is no significant difference between male and female *carolinensis* immediately east of the overlap zone. Anderson (1954), found slight dimorphism in size in the vicinity of New Orleans, Louisiana, although his measurements are not presented in a way that makes comparison with my results possible. The sexual dimorphism of *Microhyla* in size has been generally recognized and has been referred to by Hecht and Matalas (1946).

#### BETWEEN SPECIES

Male *olivacea* average very significantly smaller than all male *carolinensis* except those from Florida (fig. 1). The male *olivacea* from the overlap zone average slightly but significantly smaller than those from west of it.

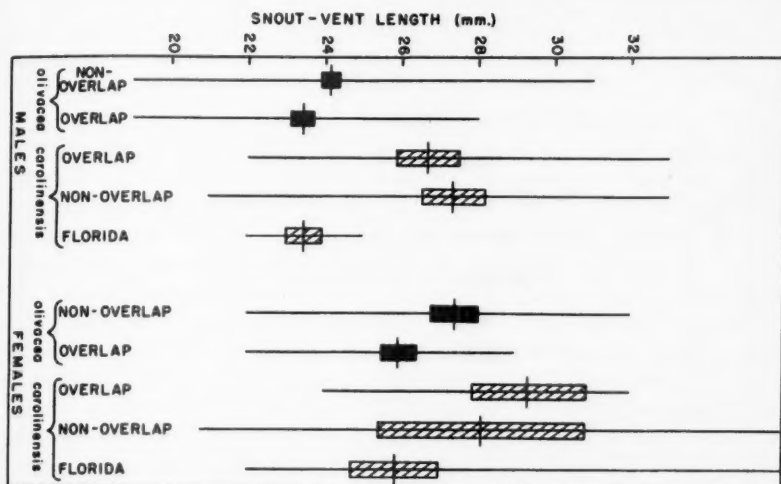


FIGURE 1. Geographic variation of male and female *Microhyla olivacea* and *M. carolinensis* in snout-vent length. Method of Dice and Leraas (1936): vertical lines show range of variation; horizontal lines show mean; boxes represent twice the standard error on each side of mean. Samples pooled in respect to overlap zone of the two species.

It is apparent that the smallest *olivacea* males and on the average the largest *carolinensis* females occur in the overlap zone, where there is the

TABLE 2.

COMPARISON OF SIZE (SNOUT-VENT LENGTH) IN MALE *MICROHYLA OLIVACEA* AND *M. CAROLINENSIS* FROM TEXAS, OKLAHOMA AND FLORIDA LOCALITIES. SAMPLES POOLED BY COUNTIES. ALL COUNTIES ARE IN TEXAS UNLESS OTHERWISE INDICATED.

<i>M. OLIVACEA</i>	Number of stations	Number of individuals	Snout-vent length with standard error
Presidio County	1	16	26.87 $\pm$ 0.40
Dawson County	1	76	25.37 $\pm$ 0.14
Travis County	7	29	24.07 $\pm$ 0.28
Gonzales County	1	94	22.81 $\pm$ 0.15
Victoria County	3	40	23.52 $\pm$ 0.23
Montgomery County	2	23	23.91 $\pm$ 0.23
Walker County	1	21	24.10 $\pm$ 0.27
Madison County	2	15	23.67 $\pm$ 0.55
<i>M. CAROLINENSIS</i>			
Montgomery County	2	14	26.21 $\pm$ 0.30
Nacogdoches County	3	26	26.65 $\pm$ 0.42
Mayes County, Oklahoma	1	16	30.31 $\pm$ 0.40
Florida (3 Counties)	3	16	23.44 $\pm$ 0.22

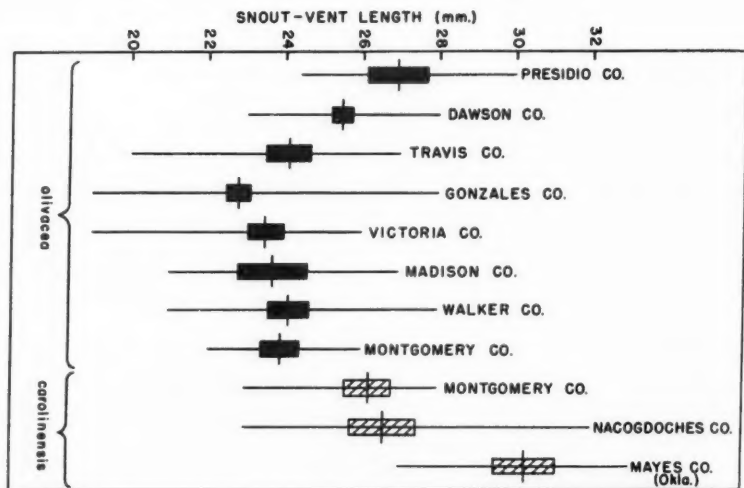


FIGURE 2. Geographic variation in male *Microhyla olivacea* and *M. carolinensis* from Texas and Oklahoma. Method of Dice and Leraas (1936). All counties are in Texas unless otherwise indicated.

possibility of cross-mating. The *olivacea* females average significantly smaller than the *carolinensis* females in the overlap zone.

#### GEOGRAPHIC VARIATION

Geographic variation is best shown by comparison of samples of males pooled on a county basis where the samples are statistically adequate (table 2). Comparison of the eight samples of *olivacea* indicates an east to west increase in body size. Four of the samples (Madison, Montgomery, Walker and Victoria counties) are from the overlap zone. The smallest males in mean length are from a locality (Gonzales County) west of the general overlap zone but where there is a disjunct, relict population of *carolinensis* also present (W. F. Blair, 1955). The sixth eastern sample is from Travis County, which is west of the overlap zone. Specimens from Dawson County, taken at the escarpment of the high plains in western Texas, average significantly larger than those in any of the eastern samples. Specimens from Presidio County, in the western part of the Big Bend in Trans-Pecos Texas, average significantly larger than the Dawson County or any of the eastern specimens.

The present evidence also shows the existence of geographic trends in body size in *carolinensis*. The Montgomery County sample, from the overlap zone, and the Nacogdoches County sample, from about 100 miles to the northeast and slightly east of the overlap zone, do not differ significantly. The specimens from Mayes County, Oklahoma, taken at the eastern border of the overlap zone and treated as being from east of it average significantly larger than those from the two Texas stations. The Florida frogs

are very significantly smaller than any of the other *carolinensis* measured.

#### DISCUSSION

The evidence now available shows that there are geographic gradients in body size in both *Microhyla olivacea* and *M. carolinensis*. The former species shows a west to east decrease in body length, while the latter shows an east to west increase. The clines are such, therefore, that the largest *carolinensis* and the smallest *olivacea*, on the average, occur in the overlap zone of the two species. This pattern of geographic variation in body size parallels the pattern of geographic variation in mating call reported by W. F. Blair (1955) in which the greatest call differences in frequency and in length occur in the overlap zone. One of these call characteristics, frequency, probably is directly related to body size, for smaller anurans of any given group tend to have a higher pitched call than larger ones of the same group. The other, length of call, appears unrelated to size.

The differences in body size, like those in mating call, belong to a complex of isolation mechanisms (W. F. Blair, 1955) which tends to restrict interspecific mating in the overlap zone of the two species. The existence of the greatest size differences as well as the greatest call differences where the two species are exposed to possible hybridization supports the argument (*op. cit.*) that these potential isolation mechanisms are being reinforced through natural selection.

The failure of Hecht and Matalas (1946) to note the size difference between the two species apparently resulted from their failure to recognize the geographic trends in size and from their consequent pooling of specimens on a species basis.

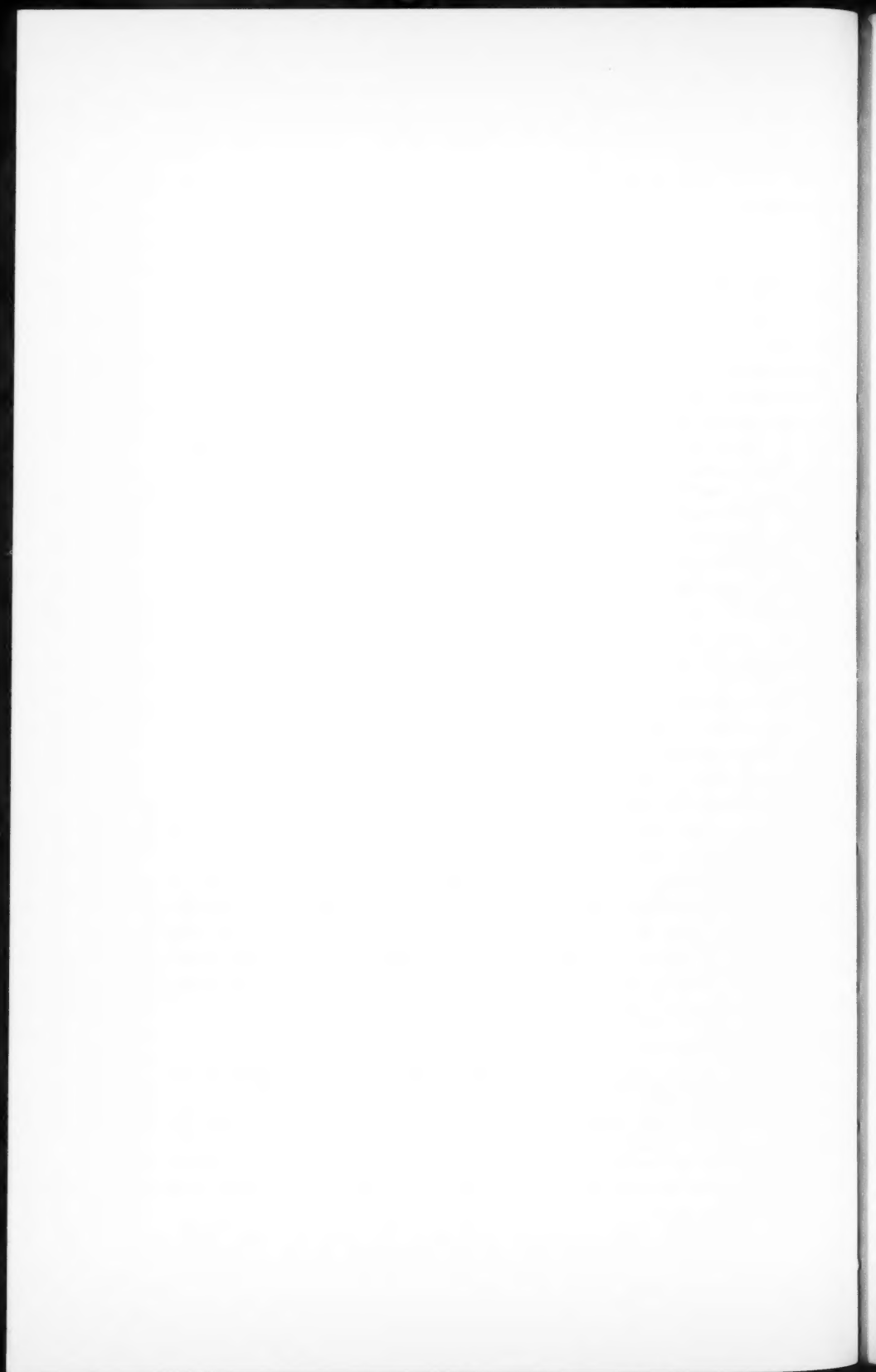
#### SUMMARY

Measurements of 659 specimens of *Microhyla olivacea* and *M. carolinensis* show that geographic gradients in size exist in both species. These gradients are such that the greatest difference in size between the two species occurs where the ranges of the two overlap. It is suggested that size difference is one of a complex of isolation mechanisms affecting interbreeding of the two species and that it and other mechanisms may be undergoing reinforcement where hybridization occurs.

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INTENSITY OF REPRODUCTIVE ISOLATION BETWEEN  
SYMPATRIC AND ALLOPATRIC POPULATIONS OF  
*BUFO AMERICANUS* AND *BUFO FOWLERI*

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INTRODUCTION

Sympatric populations can remain distinct, and be considered as species, only if gene exchange between them is limited or prevented by one or several cooperating reproductive isolating mechanisms. The distinctness of geographically separated or allopatric populations is guaranteed simply by the topographical barriers to their dispersal. Allopatric populations might or might not exhibit reproductive isolation if they were to expand their distributional ranges and overlap one another.

If two sympatric species populations are isolated solely by virtue of ecological or seasonal differences, the species gap between them may be intensified by selection in two different ways. These two methods depend upon the initial strength of the ecological or seasonal barriers. In each case, the end result may be the same; namely, the bolstering of reproductive isolation between the two species.

In the first case, if a high level of ecological or seasonal isolation prevails which precludes any possibility of hybridization, then different adaptive genes may accumulate in the contiguous stocks which may incidentally act to reinforce isolation between the two population entities. In this situation, seasonal or ecological isolation does not differ from the grosser geographical isolation, since further species-differentiation associated with both types does not imply the slightest selective advantage for reproductive obstacles to interbreeding. Different genes in the adjacent breeding units are selected for the advantage they confer upon the organisms in becoming adapted to their respective environmental conditions, rather than for any isolating effects that they may happen to possess.

The second case involves a situation where a low degree of ecological or seasonal isolation exists which permits frequent hybridization to occur. If it is assumed that the hybrids produced are at a disadvantage to the parental types in the habitats where the latter thrive best, then it would be advantageous to incorporate alleles in the respective parental genomes that would guard against the production of ill-adapted hybrids and thus prevent the wastage of reproductive energy. It would appear that this scheme of strengthening isolation operates more effectively than the mechanism outlined for the first circumstance since it involves the selection of genes for the isolating effect itself, rather than the incorporation of genes which may

secondarily have isolating effects. The implication is that isolation would be stronger between sympatric than between allopatric species (assuming that the allopatric populations can be adjudged as species). Or, if two species have overlapping distributions, isolating mechanisms should be stronger in those areas where the species are sympatric than in the noncontiguous areas. This would be particularly true if hybridization has taken place in the areas of cohabitation. The few investigations directed along these lines have suggested that selection pressure bolsters the reproductive isolation between partly or wholly sympatric species. Dobzhansky and Koller (1939) have found that some strains of *Drosophila pseudoobscura* from regions in which, or close to which, *Drosophila miranda* also occurs, show greater sexual isolation toward *D. miranda* than do certain strains of *D. pseudoobscura* geographically remote from the range of *D. miranda*. More recently, Koopman (1950) has demonstrated experimentally an increase in the amount of reproductive isolation between two species of *Drosophila* as a consequence of a systematic elimination of hybrids between the species.

The partly sympatric toad species, *Bufo americanus* and *Bufo fowleri*, offer ideal material to ascertain whether or not reproductive isolation is stronger in areas where a danger exists of hybridization. Roughly speaking, the range of Fowler's toad coincides with that of the American toad over the southern half of the range of the latter (figure 1). Habitat and seasonal

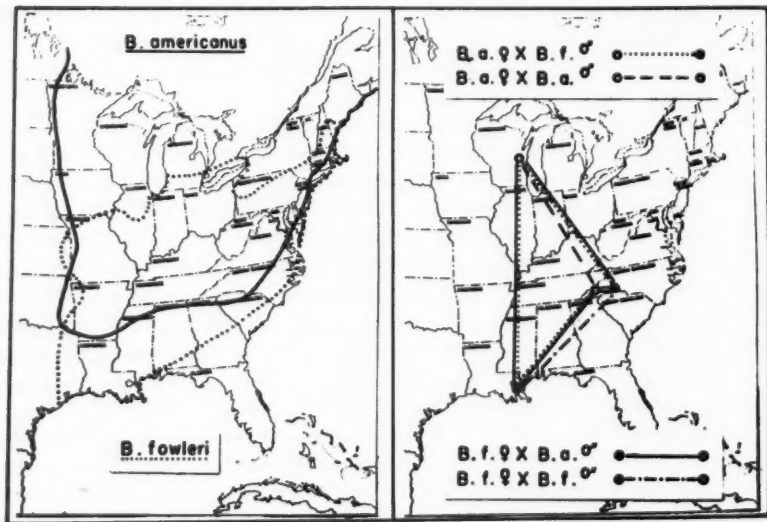


FIGURE 1. Approximate ranges of *Bufo americanus* and *Bufo fowleri* (left) and a pictorial representation of the different types of intercrosses conducted (right). The map of the range of each species was adopted from Blair (1941).

isolation tend to preserve the integrity of the two species of toads, but not in such a rigid manner as to preclude the possibility of hybridization. In any particular locality, the breeding season of *Bufo americanus* starts two

to six weeks earlier than that of *Bufo fowleri* but if it happens to extend through that of the latter, hybridization is possible, and in fact, does occur (Blair, 1941; Volpe, 1952).

The experiments herein described were conducted to determine and compare the intensity of reproductive isolation between the two *Bufo* species in areas where their ranges overlap, and in areas outside the distributional overlap of each species where opportunities for hybridization are absent. In addition, the extent to which the different populations of the same species hybridize with another related species may reflect the relative degree of divergence of the different populations of the same species. In particular, an analysis of differential characters among populations of the two species of toads may reveal a correlation between the magnitude of the differences in certain characters and the degree of hybrid incompatibility.

#### EXPERIMENTAL

##### *Laboratory hybridizations*

During the springs of 1953 and 1954, a series of artificial hybridizations were made between the two *Bufo* species from different geographical localities (cf. figure 1). Mating pairs of each species were obtained from regions where hybridization occurs with some frequency and from areas completely outside the territorial overlap. The sympatric sites chosen were Andrews, North Carolina and Shooting Creek, North Carolina. Collections of toads from both of these localities reveal some intermediate forms diagnosed morphologically as hybrids. Reciprocal intercrosses were performed among breeding adults of each species from these regions, and, in turn, these adults were crossed with *Bufo americanus* from Oshkosh, Wisconsin and *Bufo fowleri* from New Orleans, Louisiana.

Table 1 indicates the number and different kinds of crosses performed, and summarizes the results of each type of cross. A "control" cross (i.e., a fertilization with a male from the same locality, designated by a Roman numeral) was always made simultaneously with a hybrid cross (designated by a corresponding Roman numeral followed by a small letter) in order to allow accurate comparison of the development of control and hybrid embryos. Each particular control and hybrid cross was repeated at least three times (listed under the column, "No. of fertilizations"). For example, in the Experimental Set I, the eggs of six North Carolina *americanus* females were fertilized by sperm from six North Carolina *americanus* males (the control crosses, treated compositely as "I"), three Wisconsin *americanus* males (treated compositely as "Ia"), four North Carolina *fowleri* males (treated compositely as "Ib"), and five Louisiana *fowleri* males (treated compositely as "Ic"). In all cases, the control and hybrid embryos were examined at regular intervals during development at 19.4°C. from first cleavage (stage 3) to a chosen end-point, gill circulation (stage 20). The stage of development attained by the embryos and the types and proportions of abnormalities were recorded at each observation. The stages of development are defined and illustrated in Pollister and Moore (1937).

TABLE 1.  
RESULTS OF THE RECIPROCAL CROSSES BETWEEN *BUFO AMERICANUS* AND *BUFO FOWLERI* FROM VARIOUS GEOGRAPHICAL LOCALITIES.

Exp. set no.	Crosses (Conducted at 19.4°C.)	No. of fertilizations	Total no. of eggs	Died during							Total % normal at stage 20. (Mean $\pm$ S.E. and range)	Relative developmental rate (at 19.4°C.)
				Cleavage	Gastrula	Neurula	Tail bud	Muscular contraction	Heart beat	Gill circulation		
I	N. Cat. B. amer. ♀ × N. Car. B. amer. ♂	6	449	2	16	13	4	2	3	3	91 $\pm$ 1.79 (86-96)	Control
Ia	× Wisc. B. amer. ♂	3	207	1	6	9	1	1	2	2	89 $\pm$ 2.42 (87-93)	Same
Ib	× N. Car. B. fow. ♂	4	325	2	10	8	5	1	2	4	90 $\pm$ 1.15 (88-92)	Retarded slightly
Ic	× La. B. fow. ♂	5	387	7	134	41	23	10	7	5	41 $\pm$ 4.36 (28-52)	Retarded considerably
II	N. Cat. B. fowl. ♀ × N. Car. B. fow. ♂	5	369	3	14	11	3	2	1	3	90 $\pm$ 1.47 (86-93)	Control
IIa	× La. B. fow. ♂	4	322	5	8	8	3	0	1	2	92 $\pm$ 1.44 (88-95)	Same
IIb	× N. Cat. B. amer. ♂	3	210	3	5	7	1	2	1	0	91 $\pm$ 1.34 (89-93)	Accelerated slightly
IIc	× Wisc. B. amer. ♂	3	231	4	5	3	1	5	2	3	90 $\pm$ 2.04 (87-94)	Accelerated slightly

TABLE 1 (continued)

Exp. set no.	Crosses (Conducted at 19.4°C.)	No. of fertilizations	Total no. of eggs	Died during						Total % normal at stage 20. (Mean $\pm$ S.E. and range)	Relative developmental rate (at 19.4°C.)
				Cleavage	Gastrula	Neurula	Tail bud	Muscular contraction	Heart beat	Gill circulation	
III	La. B. <i>fow.</i> ♀	9	743	4	21	16	6	5	8	8	Control
IIIa	× La. B. <i>fow.</i> ♂										
IIIb	× N. Car. B. <i>amer.</i> ♂	6	490	3	13	24	118	34	17	16	Retarded considerably
IIIc	× N. Car. B. <i>fow.</i> ♂	4	330	3	10	6	3	6	2	3	Same
	× Wisc. B. <i>amer.</i> ♂	4	329	3	8	16	74	23	10	10	Retarded considerably
IV	Wisconsin B. <i>amer.</i> ♀										
IVa	× Wisc. B. <i>amer.</i> ♂	6	480	4	12	12	3	1	5	4	Control
IVb	× N. Car. B. <i>amer.</i> ♂	3	224	2	4	9	1	2	3	0	Same
IVc	× N. Car. B. <i>fow.</i> ♂	4	295	5	8	8	0	5	3	2	Retarded slightly
	× La. B. <i>fow.</i> ♂	4	298	6	98	31	18	8	4	4	Retarded considerably



The hybrid cross, North Carolina *americanus* ♀ × North Carolina *fowleri* ♂ (Exp. Set Ib) was highly successful. In four experiments,  $90 \pm 1.15$  per cent (mean and standard error of the mean) of the embryos exhibited the characteristic tadpole structure of stage 20. The greatest mortality occurred during gastrulation, but this was not associated with the effects of hybridization, since a similar mortality proportionally occurred at gastrulation in the control cross (North Carolina *americanus* ♀ × North Carolina *americanus* ♂; Exp. Set I). The reciprocal cross, North Carolina *fowleri* ♀ × North Carolina *americanus* ♂ (Exp. Set IIb) also resulted in structurally normal embryos. No evidence of severe morphological defects was observed at any time during development ( $91 \pm 1.34$  per cent of the embryos were normal in four experiments). Consequently, the gametes of the two species of toads from North Carolina are interchangeable without detrimental effects on the progeny. With respect to the time required by the hybrid and control embryos to reach gill circulation (stage 20), the developmental rates of the reciprocal hybrid embryos differed from the rate of the control embryos. The North Carolina *americanus* ♀ × North Carolina *fowleri* ♂ hybrids developed slightly more slowly than the *americanus* controls, whereas the hybrids of North Carolina *fowleri* ♀ × North Carolina *americanus* ♂ developed slightly faster than the *fowleri* controls. These differences in rate were apparently too small to offset normal development in the hybrid embryos and cause any serious abnormalities.

The outcome of the cross, Louisiana *fowleri* ♀ × North Carolina *americanus* ♂ (Exp. Set IIIa) was strikingly different from the above hybrid crosses. In six experiments, only  $54 \pm 5.45$  per cent of the embryos reached gill circulation successfully. If this hybrid cross had been conducted without a control, the low percentage of survival might have been attributable to certain experimental variables, such as an unsuitable culture medium, aged or overripened eggs, or an overcrowded condition of the embryos. The 46 per cent hybrid mortality gains significance when compared to the favorable results ( $91 \pm 0.64$  per cent of the embryos were normal) of the accompanying control cross, Louisiana *fowleri* ♀ × Louisiana *fowleri* ♂ (Exp. Set III). The cleavage stages, the gastrulation process, and neurula formation in the hybrid embryos were normal. Abnormalities in development were first noticed during the tail bud stage. In many of the hybrid embryos the body failed to elongate after neurulation and the tail bud that developed was narrow and tapered upward. The shortened body form exhibited a pronounced dorsal bending and the abdominal region was edematous and depigmented. The head structures appeared to be slightly larger than in the control embryos. These abnormalities were severe enough to cause deaths ranging from 33 to 67 per cent in the six hybrid experiments. No such defects were witnessed in the control embryos. An extremely slow rate of development of the hybrid embryos was another indication of ill-effects due to hybridization. Contrary to the results previously described in which hybrid embryos derived from the cross, North Carolina *fowleri* ♀ × North Carolina *americanus* ♂, exhibited a rapid rate of development, the combination of

Louisiana *fowleri* eggs and North Carolina *americanus* sperm resulted in a marked retardation in the developmental rate of the hybrid embryos. Similar defects and a comparable slow rate of development were also noted in hybrid embryos derived from the cross, Louisiana *fowleri* ♀ × Wisconsin *americanus* ♂ (Exp. Set IIIc). However, the cross Louisiana *fowleri* ♀ × North Carolina *fowleri* ♂ (Exp. Set IIIb) yielded structurally normal embryos.

Injurious effects were noted during the early stages of development in hybrid embryos derived from the cross, North Carolina *americanus* ♀ × Louisiana *fowleri* ♂ (Exp. Set Ic). The first definite indication of hybrid defects appeared during gastrulation. The dorsal blastopore lip of the hybrid was more heavily pigmented and undercut the embryo more deeply than in the control. As the abnormal blastopore lips encircled the hybrid gastrula, a large share of the yolk failed to become incorporated within the embryo. Most of the embryos with extruding yolk plugs cytolized. Irregularities in the later stages of development were not evident, and a total of  $41 \pm 4.36$  per cent of the hybrid embryos reached stage 20 successfully. The same types and proportions of early defects were also noted in hybrid embryos obtained from the cross Wisconsin *americanus* ♀ × Louisiana *fowleri* ♂ (Exp. Set IVc). In marked contrast, no abnormalities were noticed in embryos of the cross North Carolina *fowleri* ♀ × Louisiana *fowleri* ♂ (Exp. Set IIa).

Of considerable interest was the outcome of the reciprocal crosses between North Carolina *fowleri* and Wisconsin *americanus* (Exp. Sets IIc and IVb). It might have been expected that this combination would be as unfavorable as the reciprocal crosses involving Louisiana *fowleri* and Wisconsin *americanus* (or North Carolina *americanus*). This was not the case. As far as could be determined, the intercross of a North Carolina *fowleri* ♀ and a Wisconsin *americanus* ♂, and the reciprocal cross, were perfectly harmonious. In fact, the Wisconsin *americanus* behaved in an identical manner in the hybridization experiments as a North Carolina *americanus*. A comparison of hybrid developmental rates revealed that embryos of the North Carolina *fowleri* ♀ × Wisconsin *americanus* ♂ cross developed at the same rate as hybrid embryos derived from the cross, North Carolina *fowleri* ♀ × North Carolina *americanus* ♂.

The hybridization experiments described in this section may be summarized and interpreted as follows: Crosses between sympatric populations of the two *Bufo* species from North Carolina, where a potential and actually realized danger of hybridization exists, were far more successful than crosses between *certain* allopatric populations of the two species. A partial hybrid inviability has been demonstrated in the reciprocal crosses between Louisiana *fowleri* and North Carolina *americanus*. The latter finding supports Muller's contention (1942) that isolating mechanisms may arise as a by-product of genetic divergence of allopatric populations. However, not all genetic differences that accumulate in geographically separated populations of a species are associated with isolating effects, as demonstrated by the harmonious combination of a Wisconsin *americanus* and a North Carolina *fowleri*. It may be inferred that both the geographically separated

Wisconsin *americanus* and Louisiana *fowleri* populations are changing genetically through mutations and random fluctuations in gene frequencies, but that the gene complexes in the Louisiana *fowleri* population are not only adaptively important to the organisms themselves, but have secondarily or incidentally weak isolating effects.

#### *Embryonic Rates of Development*

If we adhere to the evolutionary tenet that an isolating mechanism originates as a by-product of genetic differentiation, then the genes responsible for the initial development of hybrid inviability were not selected for the effect of isolation, but were selected because they imparted greater survival value to the organisms in their specific environments. The inference is that the particular genes have pleiotropic effects, and some of these effects may be expressed in certain conspicuous morphological traits or may be disclosed in various physiological processes. Attempts to seek out the manifold expressions of the "isolating" genes would necessarily involve searching for testable characters that are unique to the Louisiana *fowleri* population, and are completely different from those characters appearing in both the Wisconsin and North Carolina *americanus* populations. Since the hybrid malformations in the Louisiana *fowleri*  $\times$  North Carolina (or Wisconsin) *americanus* crosses are first evident in the embryonic stages and the ill effects appear to be related to a disturbed developmental rate in the hybrid embryos, it seemed appropriate to test at least one embryonic process, namely, embryonic rate of development, as a possible underlying factor responsible for hybrid inviability. As shown below, the magnitude of the differences in embryonic rate of development among the various toad populations parallels strikingly the degree of hybrid compatibility.

The rate of development of fertilized eggs from mating pairs of toads from each of the localities involved in the present study was determined by examining the embryos at each of several constant temperatures at regular intervals from first cleavage (stage 3) to a chosen end-point, gill circulation (stage 20).<sup>1</sup>

The data on rate of development are plotted for comparisons in figures 2, 3, and 4. *Bufo americanus* embryos from North Carolina develop faster than *Bufo fowleri* embryos from North Carolina (figure 2). At each temperature tested, the North Carolina *americanus* embryos reached the experimental end-point, stage 20, in less time than that required by North Carolina *fowleri* embryos. It is of interest to note that the slope of the rate curves for both types of embryos are almost identical, which indicates that degree changes in temperature affect the developmental reactions of both types of embryos in a similar manner. This may be the basis for the compatibility witnessed in the hybrid crosses between the two species from the North Carolina populations.

<sup>1</sup>A more detailed account of embryonic rate of development of several toad species from different localities can be found in Volpe (1953).

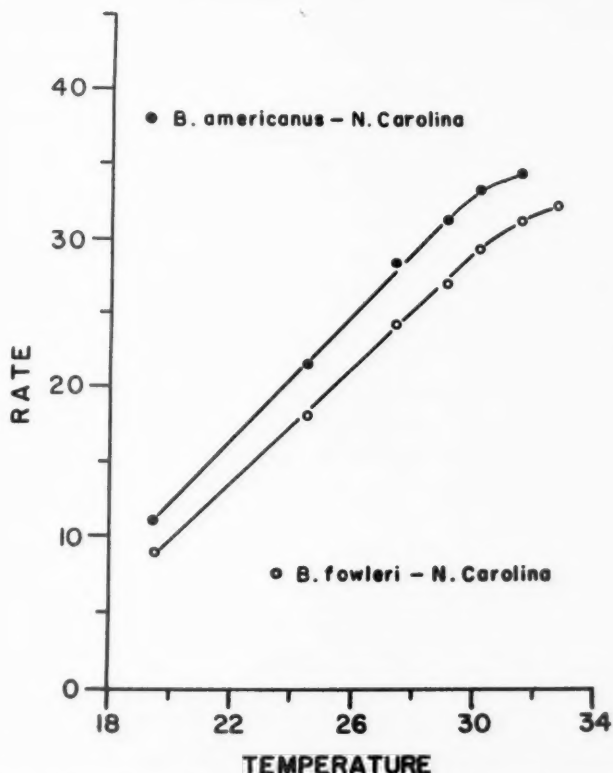


FIGURE 2. A comparison of the rate of development of eggs of *Bufo americanus* from North Carolina and *Bufo fowleri* from North Carolina. The ordinate represents the rate of development or 1,000 divided by the time in hours between stages 3 and 20; the abscissa, the temperature in °centigrade.

As shown in figure 3, the rate of development of Wisconsin *americanus* embryos is identical with that of North Carolina *americanus* embryos. The parallel behavior of North Carolina and Wisconsin *americanus* when crossed with *fowleri* from Louisiana (or North Carolina) may be causally associated with the identical rates of development of North Carolina and Wisconsin *americanus*.

As illustrated in figure 4, the slope of the rate curve of Louisiana *fowleri* embryos is decidedly different from that of the other toad embryos examined. It is tempting to suggest that an asynchronous developmental rate in the hybrid embryos between Louisiana *fowleri* and North Carolina (or Wisconsin) *americanus* is the factor initially responsible for the observed hybrid abnormalities. One difficulty apparent in this explanation lies in the successful outcome of the reciprocal crosses, Louisiana *fowleri* × North Carolina *fowleri*. Nevertheless, it should be noted that the rate curves of the Louisiana and North Carolina *fowleri*, although different, actually

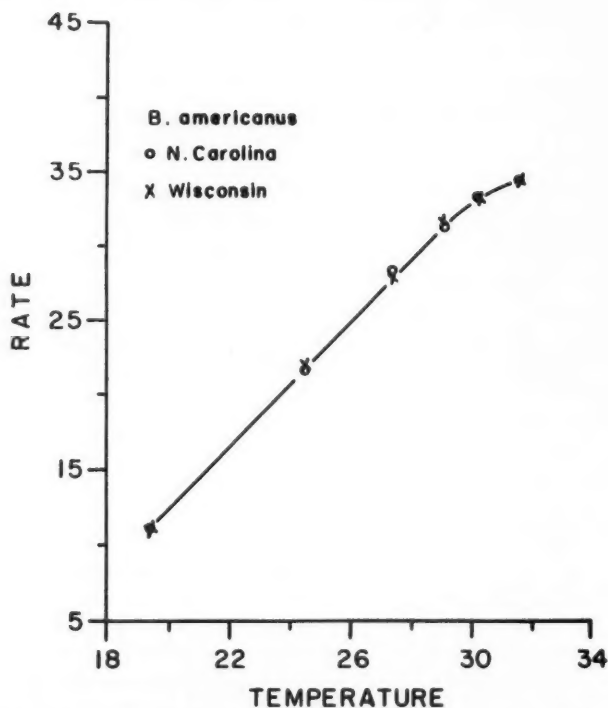


FIGURE 3. A comparison of the rate of development of eggs of *Bufo americanus* from North Carolina and Wisconsin. Co-ordinates as in Figure 2.

approach one another at the low temperatures at which the hybridization experiments were conducted. In essence, it may be that the rates of development of the foregoing parental forms are not sufficiently different at low temperatures to cause abnormalities in the hybrid embryos. The partial failure of hybrid embryos between Louisiana *fowleri* and North Carolina *americanus* may be attributable to the fact that the rate curve of Louisiana *fowleri* is most divergent from the rate curve of North Carolina *americanus* at 19.4°C., the same temperature at which the hybridization experiments were conducted. If the interpretation is valid that conflicting modes of action of temperature-related processes in the developing hybrid embryo play an important role in hybrid compatibility, then it is conceivable that the intercrosses between Louisiana *fowleri* and North Carolina *americanus* would be more successful at the higher temperatures (where their rate curves converge). This aspect is within the bounds of future investigation.

#### DISCUSSION

In the introduction, the concept was advanced that isolating mechanisms should be more rigid between two species in areas of distributional overlap

where a danger exists of hybridization than in the noncontiguous areas. The experimental results in the present investigation indicate contrarily that hybrids derived from crosses among certain allopatric populations of the two *Bufo* species investigated are inferior in viability to hybrids derived from sympatric representatives of the two species. Thus, intrinsic isolating mechanisms have not developed to reinforce the extrinsic isolating barriers that separate the two toad species in the areas of cohabitation examined, and in contradistinction, the earliest traces of intrinsic isolation have developed in certain geographically separated populations.

The finding that reproductive isolation is weaker between sympatric than between allopatric species populations is not as exceptional as it may appear. Several *Drosophila* investigators (Mainland, 1942; Wharton, 1942; Spieth, 1951) have found that certain strains of particular *Drosophila* species displayed greater sexual isolation toward one another as the geographical distance between the strains increased. Mainland (1942) has studied the *Drosophila funebris* group and has concluded that "those strains of *D. macrospina* originating from areas closer to that inhabited by *D. subfunebris* were inclined to show less sexual isolation to *D. subfunebris* than

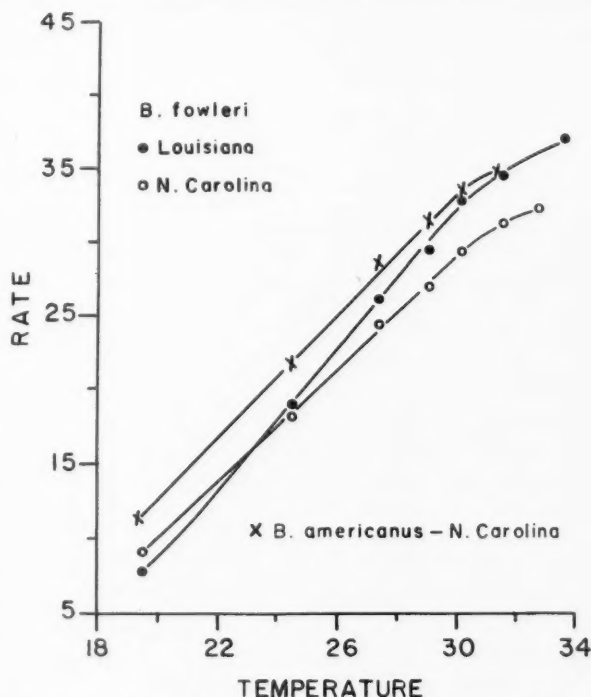


FIGURE 4. A comparison of the rate of development of eggs of *Bufo americanus* from North Carolina and *Bufo fowleri* from North Carolina and Louisiana. Co-ordinates as in Figure 2.



those coming from more remote localities." Spieth (1951) has examined the mating behavior of fourteen strains of the *D. virilis* group, and has found that at both the courtship and copulation levels, there was greater discrimination between certain strains of two species as the point of origin of the strains involved increased. In other groups of animals, Kawamura (1953) investigating four species of the salamander genus, *Hynobius*, in Japan has found a few exceptions to the supposition that isolation is more complete between two species populations having adjacent distribution areas. As an instance, *H. nebulosus* from Okayama produced more abnormal larvae by mating with the more distant Niigata *H. nigrescens* than the adjacent *H. nigrescens* from Toyama. Hubbell's (1936) monographic revision of the cave cricket genus, *Ceuthophilis*, has revealed a few species relationships which appear to parallel the above findings. Thus, the expected strong correlation between the geographical proximity of species populations and the degree of isolation between them has not been realized in quite a few cases.

Several phases of the present investigation require explanation—the lack of intrinsic isolation between *B. americanus* and *B. fowleri* in the hybrid areas, the development of genes with weak isolating effects in Louisiana *B. fowleri*, and the absence of demonstrable isolating genes in Wisconsin *B. americanus*. Dobzhansky (1951) advanced the thesis that natural selection would strengthen isolation between two sympatric species until the possibility of gene exchange between these species is severely limited or stopped. The apparent provision in this theory is that the two groups must have diverged previously to such an extent that the initial hybrids formed are less viable than the parental types, partly sterile, or less well adapted for any available habitat. In other words, it appears that natural selection may reinforce isolating mechanisms that have already resulted in some wastage of reproductive energy of each species. If, however, two sympatric species are isolated merely by extrinsic barriers (e.g., differences in breeding seasons or habitat preferences), and the hybrids between them are not at a selective disadvantage to the parental types, then the stimulus for natural selection to reinforce isolation is lacking. In the North Carolina hybrid areas, either reproductive isolation has not been strengthened by selection since no loss of fitness results from intercrossing, or the two groups of toads are newly in contact and selection has not as yet operated (assuming that the hybrids produced are in some way, as yet undetected, ill-adapted).

The development of genes with weak isolating effects in Louisiana *fowleri* is probably a by-product of genetic adaptation to local environmental conditions. This explanation presupposes that the Louisiana *fowleri* have been unexposed to the possibility of hybridization with *americanus* or a stock related to *americanus*. *Bufo americanus* is replaced in the southeastern states by a close relative, *Bufo terrestris*. The latter extends into the southeastern parishes of Louisiana. It may be argued that past hybridization between Louisiana *fowleri* and Louisiana *terrestris* (assuming that it

has taken place) has led to the establishment of "hybrid inviability" genes in Louisiana *fowleri*. This viewpoint is weakened by the demonstration that hybridization between North Carolina *fowleri* and North Carolina *americanus* has not promoted the development of intrinsic isolating genes in North Carolina *fowleri*. One would assume that if past hybridization between Louisiana *fowleri* and Louisiana *terrestris* (the *americanus*-like stock) has been instrumental in establishing genes with isolating effects in Louisiana *fowleri*, then past hybridization between North Carolina *fowleri* and North Carolina *americanus* should also have been an important agent in incorporating isolating alleles in the North Carolina *fowleri*. The interpretation which involves the fewest assumptions is that the "hybrid inviability" genes in Louisiana *fowleri* have not developed for their usefulness as an isolating mechanism, but have developed incidental to the process of divergence.

The demonstration that similar incidentally-acting isolating genes have not accumulated in Wisconsin *americanus* may indicate that selection pressures differ, or that the Wisconsin population is a phylogenetically younger stock and genetic differentiation has not proceeded as far as in the Louisiana population. With respect to the latter point, it is generally acknowledged that southerly distributed populations of both *americanus* and *fowleri* are closer to their centers of origin than the more northerly distributed populations.

The two Bufo species have been found to breed side by side in certain areas, and it has been demonstrated that the hybrids are viable and fertile (Blair, 1942) and are maintained in nature (Volpe, 1952). These findings suggest that the two species of toads had been selected in the past during a period of geographical separation for different ecological situations which have since coalesced in many areas of the broad overlap zone. The speciation process apparently was not completed during the period of geographical isolation. Indeed, the fact that we discern now the first sign of intrinsic isolating genes developing in the Louisiana *fowleri* population may indicate that the former initial geographical separation between the two groups of toads was not of a sufficiently long period of time to achieve marked species differentiation. It is also equally probable that the two toad groups may have been previously separated for a great interval of time, but the two groups did not diverge in characters which would prove valuable later in causing hybrid incompatibility. Geographical isolation does not automatically guarantee genetic divergence with concomitant reproductive isolation.

The lack of sterility between sympatric representatives of the American and Fowler's toads, the breakdown of ecological barriers in certain areas, and the apparent successful survival of hybrids in nature raise the question as to the systematic validity of designating the two groups as species. The distribution of *fowleri* and *americanus* is not that generally considered characteristic of geographic races (subspecies), since their ranges overlap widely in the mid-eastern part of the United States (figure 1). The situation may be explained as either a vast intergradation of races somewhat

ecologically distinct, or as hybridization of two species once separated and newly in contact over a large area. Critical evidence in support or refutation of these two alternatives is lacking. The critical question to be answered is not whether the two groups exchange genes (in fact they do), but to *what extent* they exchange genes in the entire area of overlap. The few areas examined and reported by various workers (Miller and Chapin, 1910; Hubbs, 1918; Myers, 1927; Pickens, 1927; Blair, 1941; Volpe, 1952) have revealed natural hybridization between the two groups, but detailed field and laboratory studies must be conducted throughout the entire range of overlap to ascertain the extent to which the discontinuities between the two groups have been blurred by hybridization. In view of the uncertainties involved, and the absolute distinction between the two types in the non-overlap areas, *americanus* and *fowleri* are here treated, with certain misgivings, as species. For the present, the occurrence of successful hybridization between sympatric representatives of the two species of toads serves best to emphasize the transiency of extrinsic isolating mechanisms.

#### SUMMARY

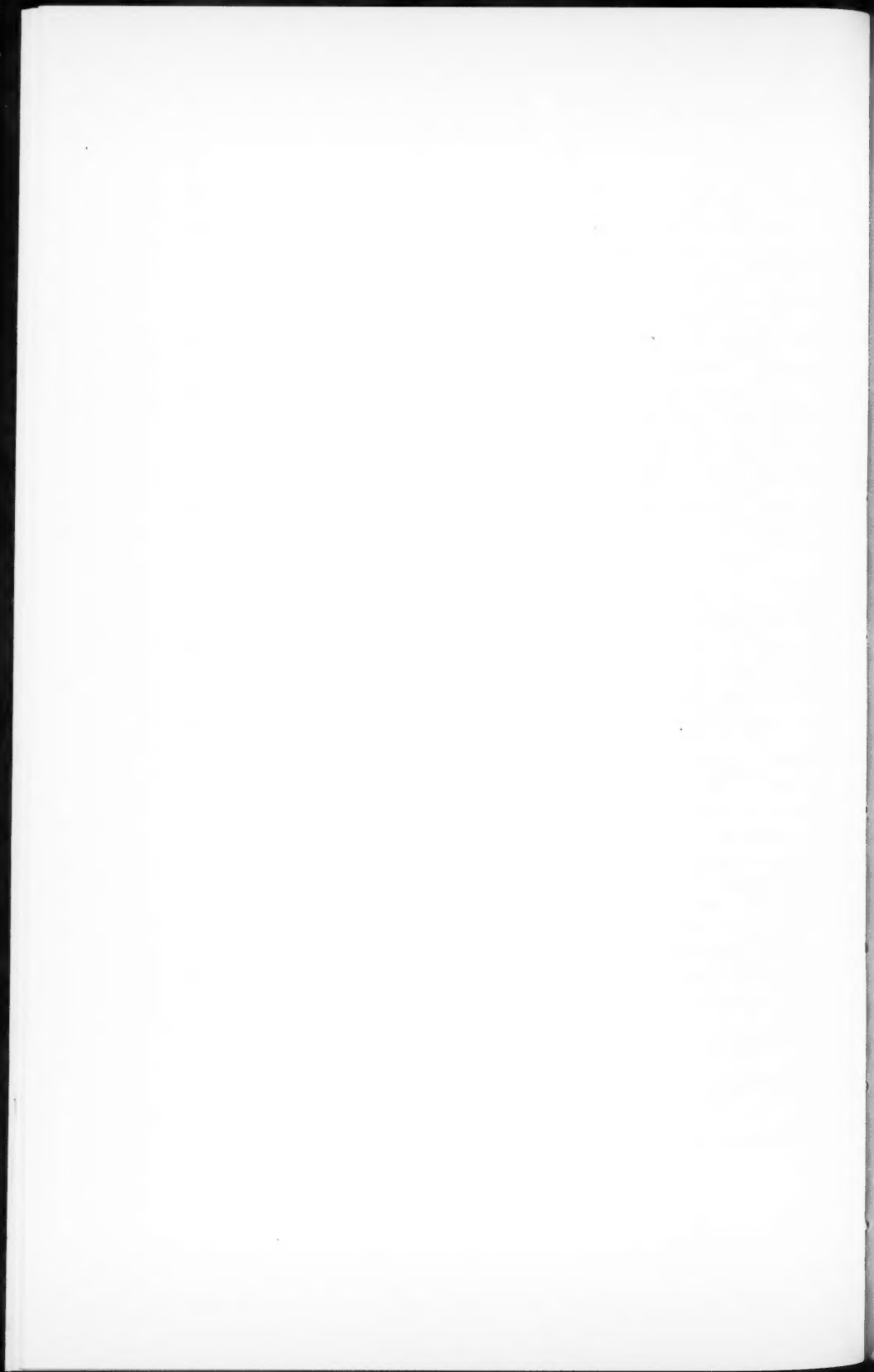
Hybrid crosses were conducted between different geographical representatives of the two partly sympatric species of toads, *Bufo americanus* and *Bufo fowleri*, to test the applicability of two evolutionary tenets; namely, Muller's contention that the initial signs of reproductive isolation originate as by-products of adaptation, and the postulate, first advanced by Dobzhansky and Koller, that reproductive isolation should be stronger between two species in the area of cohabitation than in the noncontiguous localities. The experimental results of the various intercrosses have indicated that genetical differentiation in certain geographically separated populations of toads has been associated with the early development of isolating mechanisms, and that no positive correlation exists between the territorial adjacency of the two species and the degree of reproductive isolation between them. In particular, crosses between sympatric populations of the two *Bufo* species from North Carolina, where natural hybridization occurs with some frequency, were far more successful than crosses between certain allopatric populations of the two species. A partial hybrid inviability has been demonstrated in crosses between *B. fowleri* from Louisiana (where only *fowleri* occurs) and *B. americanus* from North Carolina. However, there were no traces of hybrid incompatibility in crosses between *B. americanus* from Wisconsin (where only *americanus* occurs) and *B. fowleri* from North Carolina.

#### ACKNOWLEDGMENTS

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Tinbergen, Niko, 1954. *The herring gull's world. A study of the social behavior of birds*. 256 p., 30 plates, 58 figures. \$4.00. Frederick A. Praeger, New York.

This is another substantial contribution by the publishers of the New Naturalist series. Well written, handsomely illustrated, and with a pleasing format, these monographs on diverse biological topics provide a readable, essentially non-technical introduction to their subject matter. This new volume is a highly interesting account of Tinbergen's studies of the herring gull, illustrating methods and theory of the European school of comparative ethologists. Beginning with an introduction to the aims of animal behavior studies, the author then treats of aspects of the bird's sensory and locomotor organs, non-reproductive behavior, formation of the colony, mating, family life, incubation, and the chick's world. Relevant studies on other animals are drawn upon. A fairly large bibliography and a final chapter summarizing the results of his efforts and suggesting directions for further research enhance the value of the book. The technically excellent photographs are remarkable in that Tinbergen has succeeded in recording the gulls in the behavioral movements of which he writes. Thus, the plates are made an integral



part of the text. Tinbergen's genuine enthusiasm for his subject will undoubtedly stimulate others. Indeed, more research may help meet recent criticisms of the methods and concepts of these innate behavioral studies.

D. M.

White, M. J. D., 1954. *Animal cytology and evolution*, second edition. xiv and 454 p., 146 text figures. \$8.50. Cambridge University Press, New York.

The second edition of this widely known work is more than a revision designed to include new research on animal cytology during the past ten years, although this function is admirably performed. In line with other modern writers on evolution, Dr. White has increased his efforts to show connections between the observed phenomena which he reviews and basic principles of evolutionary dynamics, particularly genetic recombination and selection. The adaptive significance of polymorphism for chromosomal inversions, as demonstrated by Dobzhansky and his followers, is accepted and well reviewed, and a similar significance is considered to exist for the more complex and less well understood chromosomal polymorphism in the Orthoptera. Supernumerary chromosomes are considered to be adaptive in most instances, but the nature of their adaptive value is not yet clear. In regard to the other phenomena which are the subject of the greater part of Dr. White's book; namely, the great diversity of chromosome numbers and form, the strange modifications of meiosis and the chromosome cycle which occur in certain insects, and the bewildering array of cytological devices which govern sex determination, the author can only suggest that the evolution and persistence of these phenomena is difficult or impossible to explain unless we assume that natural selection has played an important role.

The final chapter, which bears little resemblance to the concluding chapter of the first edition, marks Dr. White's book as a milestone in the progress of our understanding of the relation between cytogenetic processes and evolution. This book is the first to accept as generally recognized the role of natural selection as the force which acts on hereditary variation to produce directed evolutionary change, and to point out clearly that the next task of the cytogeneticist is to demonstrate how each of the diverse cytogenetic mechanisms or genetic systems aids in adapting the organisms possessing it to the particular environmental conditions which they face, or which their ancestors faced in the past. Dr. White does not attempt hypothetical speculations to explain these mechanisms, but rather emphasizes the need of more complete knowledge before valid hypotheses can be formulated. One can only hope that cytogeneticists who re-read this book in its new edition, or that the younger scientists not familiar with Dr. White's earlier work, will see and accept his challenge, and will raise cytogenetics to even greater heights as a means of explaining evolution.

G. LEDYARD STEBBINS

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